# Development of dorsal stream functioning in biological and structure-from-motion perception in 5-7 year old children

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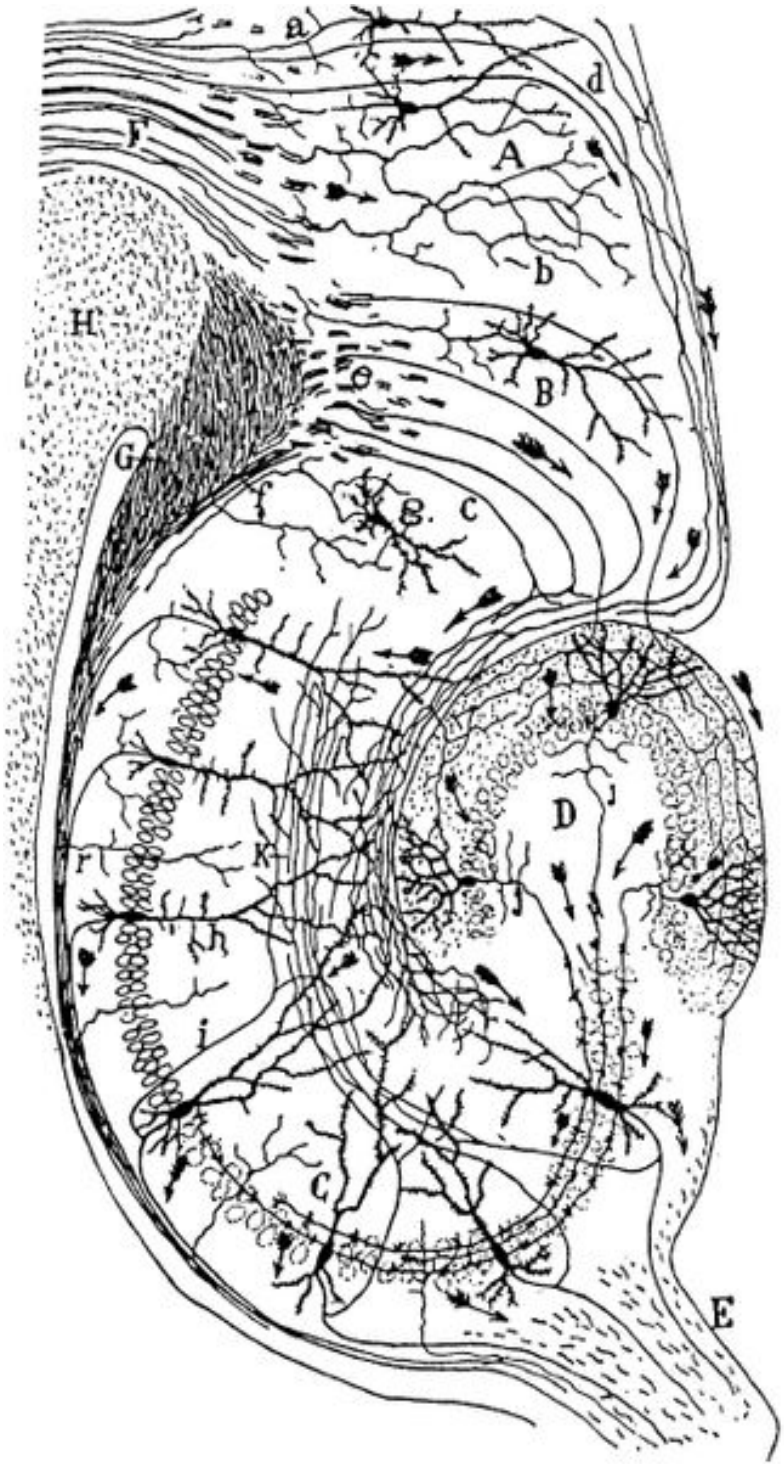
*"If a solution fails to appear after all of this, and yet we feel success is just around the corner, try resting for a while.... Like the early morning frost, this intellectual refreshment withers the parasitic and nasty vegetation that smothers the good seed. Bursting forth at last is the flower of truth."*

*Santiago Ramon y Cajal "Advice for young investigators", 1897, 1st edition*



# Contents

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# Summary

Motion perception is a fundamental aspect of vision, serving a number of important perceptual, behavioral and cognitive functions. Normal development of the visual motion system is, therefore, most relevant for the overall perceptual and cognitive development of a child. From birth, children are sensitive to visual motion. Thereafter, the perceptual skills for visual motion detection continue to improve throughout childhood and adolescence. Understanding the maturation of visual motion processing in normal-achieving children will help to define the neuronal basis for atypical perceptual and cognitive development.

The main goal of this thesis was to investigate the neural development of normal-achieving children using functional magnetic resonance imaging (fMRI) during perception of structure-from-motion (SFM) and biological motion (BM) tasks. The SFM task consisted of randomly moving point-light dots (RM), coherently moving dots that formed a 3D rotating object (SFM) and static dots. Biological motion describes the patterns of movement generated by living forms. During the BM experiment, subjects performed a perceptual task with BM, BM in snow (BM_s) using coherently moving background noise as distractors and equivalent scrambled motion (SM/SM_s) stimuli. There is evidence from studies with adult subjects that tasks involving these different motion-based discriminations activate distinct specialized brain areas.

In the first study (chapter 2) the development of neuronal correlates involved in SFM perception task, specifically the role of dorsal and ventral stream maturation, was investigated. In adults (age 20-30 years) the perception of RM elicited increased neural activity as compared with static dots in motion processing related visual areas, including visual area 3a (V3a) and middle temporal area (hMT+). Children (age 5-6 years) showed less pronounced activity in area V3a than in adults. SFM perception induced enhanced neural activity as compared to RM in adults in the left parietal shape area (PSA), whereas children showed increased neural activity within dorsal (V3a) and ventral brain areas (lingual gyrus) of the occipital cortex. Enhanced activity in specialized areas within the dorsal pathway during RM perception (V3a) and SFM perception (PSA) was only found in the mature adult brain. Secondly, we found a developmental shift in neural activity from low level shape and motion specialized areas in children, including partially immature area V3a, to high order areas in the parietal lobule (PSA) in adults.

In the second study (chapter 3) the development of neural correlates involved in BM perception were explored. The perception of BM in adults has been associated with neural activity in the right posterior superior temporal sulcus (pSTS) representing a pivotal point of the dorsal and ventral stream. During BM perception adults (age 20-32) showed increased activation in dorsal (cuneus, precuneus and supramarginal gyrus) and ventral areas (lingual gyrus, fusiform gyrus and hMT+) of the visual system as well as in pSTS predominately in the right hemisphere. Children (age 5-7 years) only activated the right fusiform gyrus for the same condition. Group comparisons indicated increased activation in right pSTS and bilateral parietal regions in adults for BM perception. Likewise children showed enhanced activation in fronto-parietal regions of the left hemisphere when BM_s was presented. Thus, only adults activated the expected dorsal and ventral regions including pSTS during BM perception, whereas children seem to recruit networks within the ventral stream. Furthermore, only children engaged dorsal (parietal) and frontal regions during task conditions with increased level of attention such as in the perception of BM in snow.

These two developmental studies both revealed that task-specific dorsal stream of the occipital cortex and parietal lobule functioning is not mature at age six. The present results also support the hypothesis that age dependent neural activity rely upon the complexity of the motion stimulus and that high order processes are substituted by low order processes in the immature brain. Furthermore, children engaged task-unspecific areas in task conditions with increased level of attention. Activations of these areas may serve as compensational processes of an otherwise immature network.

# Zusammenfassung

Die Bewegungswahrnehmung spielt für zahlreiche Funktionen der visuellen Wahrnehmung sowohl auf Verhaltens- als auch auf Kognitionsebene eine fundamentale Rolle. Man kann daher davon ausgehen, dass bei Kindern die normale Entwicklung der visuellen Bewegungswahrnehmung von grundlegender Bedeutung für die visuelle und kognitive Gesamtentwicklung ist. Schon bei Neugeborenen lässt sich eine Sensitivität für visuelle Bewegung erkennen. Die visuellen Fähigkeiten verbessern sich jedoch kontinuierlich bis zur Adoleszenz. Das Verständnis der Reifung des visuellen Systems von sich normal entwickelnden Kindern wird später helfen, die neuronale Basis atypischer Entwicklung der Wahrnehmung und Kognition zu definieren.

Das Ziel dieser Dissertation war die Untersuchung der neuronalen Entwicklung von sich normal entwickelnden Kindern. Die Probanden wurden während dem Lösen von Wahrnehmungsaufgaben mit structure-from-motion (SFM) und biological motion (BM) Stimuli mittels der funktionellen Magnetresonanztomographiemethode (fMRT) untersucht. Die SFM Aufgabe bestand einerseits aus sich zufällig bewegenden Lichtpunkten (random motion - RM) und andererseits aus Lichtpunkten, die sich kohärent bewegten und dabei ein dreidimensionales Objekt abbildeten (SFM), sowie statischen Punkten als Baseline. Während dem Experiment zur biologischen Bewegungswahrnehmung führten die Probanden eine Wahrnehmungsaufgabe mit vier verschiedenen Stimuli aus. Die biologische Bewegung wird dabei als Bewegung bezeichnet, die von Lebewesen generiert wird. Einerseits bewegten sich die Lichtpunkte biologisch (BM) oder die biologische Bewegung wurde (BM in snow - BM_s) „im Schneesturm" präsentiert, wobei sich im Hintergrund Lichtpunkte als Distraktoren kohärent bewegten. Zusätzlich wurden Stimuli gezeigt, die durch die randomisierte Anordnung der Lichtpunkte aus den biologischen Stimuli entstanden sind (scrambled motion - SM/SM_s). Aus Studien mit erwachsenen Probanden ist bekannt, dass solche Aufgaben Areale im Gehirn zu aktivieren vermögen, die spezifisch Bewegung verarbeiten.

In der ersten Studie (Kapitel 2) wurde die Entwicklung der neuronalen Korrelate bei einer SFM Aufgabe, insbesondere die Rolle des ventralen und dorsalen Pfades innerhalb des visuellen Systems untersucht. Bei den Erwachsenen wurden bei der Wahrnehmung von RM (verglichen mit SM) Areale wie V3a und der mittlere

Temporallappen (hMT+) aktiviert, die namhaft an der Verarbeitung von bewegten Stimuli beteiligt sind. Im Gegensatz dazu zeigten die Kinder (5-6 Jahre alt) eine weniger ausgeprägte Aktivierung im Areal V3a. Während bei den Erwachsenen die Wahrnehmung von SFM verglichen mit RM eine Aktivierung im linken parietalen Formareal (parietal shape area – PSA) hervorrief, zeigten die Kinder nur Aktivität in dorsalen (V3a) und ventralen Gehirnregionen (lingualer Gyrus) des Okzipitallappens. Bei der Wahrnehmung von RM (V3a) und SFM (PSA) wurde eine verstärkte Aktivierung in dorsalen Regionen nur im reifen Erwachsenengehirn gefunden. Zudem fanden wir bei Kindern eine entwicklungsabhängige Verlagerung der neuronalen Aktivierung aus niedrigen form- und bewegungsspezifischen Arealen wie dem teilweise noch unreifem V3a, zu parietalen sprich höheren Arealen wie PSA bei Erwachsenen.

In der zweiten Studie (Kapitel 3) wurde die Entwicklung der neuronalen Korrelate im Zusammenhang mit der Wahrnehmung von biologischen Bewegungen untersucht. Bei Erwachsenen geht die Wahrnehmung von BM mit neuronaler Aktivität im rechten posterioren superioren temporalen Sulcus (pSTS) einher. Diese Region wird als Dreh- und Angelpunkt des ventralen und dorsalen Pfades betrachtet. Während der BM Wahrnehmung zeigten die Erwachsenen (20-32 Jahre) erhöhte Aktivierung in dorsalen (Cuneus, Präcuneus und supramarginalem Gyrus) und ventralen Gebieten (lingualer und fusiformer Gyrus sowie hMT+) sowie dem pSTS vorwiegend in der rechten Hemisphäre. Die Kinder (5-7 Jahre alt) aktivierten bei demselben Stimulus nur den rechten fusiformen Gyrus. Gruppenvergleiche ergaben bei Erwachsene eine erhöhte Aktivierung im rechten pSTS und in bilateralen parietalen Region während der BM Wahrnehmung. Gleichermassen zeigten Kinder eine erhöhte Aktivierung in fronto-parietalen Gebieten innerhalb der linken Hemisphäre bei der Präsentation von BM_s. Folglich aktivierten während der BM Wahrnehmung nur die Erwachsenen die erwarteten dorsalen und ventralen Gebiete inklusive pSTS während die Kinder eher ventrale Gebiete zu rekrutieren schienen. Des weiteren zeigten nur die Kinder zusätzliche Aktivierungen in dorsalen (parietalen) und frontalen Gebieten während der BM_s-Aufgabe, die eine erhöhte Aufmerksamkeit erforderte.

Diese zwei Entwicklungsstudien zeigten beide, dass die aufgabenspezifische Funktion des dorsalen Pfades im Okzipital- und Parietallappen im Alter von 6 Jahren noch nicht voll ausgereift ist. Die aktuellen Ergebnisse unterstützen zudem die

Hypothese, dass die altersabhängige Aktivierung von der Komplexität des bewegten Stimulus abhängt. Des weiteren konnte gezeigt werden, dass Prozesse, die im reifen Gehirn auf hierarchisch hohem Niveau verarbeitet werden, im unreifen Gehirn auf einer tieferen Stufe ablaufen. Ausserdem zeigten Kinder eine zusätzliche aufgabenunspezifische Aktivierung sobald die Aufgabe erhöhte Aufmerksamkeit erforderte. Aktivierungen in diesen Arealen können als Kompensationsprozesse für ein ansonsten noch unreifes Netzwerk verstanden werden.

# 1 Introduction

Humans rely on vision more than on any other sensory input. 20% of the human brain is involved in visual processing and more is devoted to visual thinking than to any other form of sensory input.

The detection of motion is one of the most pervasive features of the visual system. In every species where neuroscientists have looked for visual motion sensitivity—from flies (Egelhaaf and Borst 1993), beetles (Hassenstein and Reichhardt 1956), crabs (Zeil and Zanker 1997) and frogs (Barlow 1953), to rabbits (Barlow and Hill 1963), cats (Hubel and Wiesel 1962) and primates (Hubel and Wiesel 1968) — it has been found. Motion detection is basic to perception, cognition and action. It contributes to a great range of visual functions, including scene segmentation, depth perception, postural and oculomotor stabilization, recognition of characteristic kinematic events such as the actions of other individuals, and the control of actions in dynamic situations. Moving targets have a high salience in attracting attention in the peripheral visual field. Motion is continuously present in the visual image, through eye movements, self-motion, and the motion of external objects. We expect, therefore, that the development of visual motion processing will be a very important part of the overall development of vision in infancy and childhood.

Since vision provides the sensory input needed for many higher cognitive functions, the maturation of the visual system plays an important role in the overall cognitive development of a child. Children use visual motion information to learn and improve perceptual and also behavioral skills. Likewise, children learn motor actions by the observation and subsequent imitation of body movements (Cochin, Barthelemy et al. 2001). Furthermore, it has been suggested that in young children dynamic perceptual cues are particularly important for the categorization of objects and living creatures (Mak and Vera 1999).

The normal development of basic visual functions is a prerequisite that this learning can occur. Although many visual abilities are functional early in life, perceptual skills continue to improve throughout childhood and even adolescence. During development new networks emerge, connections are built, and information processing gets faster and more efficient. These plastic changes reflect functional

brain maturation and can be investigated by brain mapping technologies, such as functional magnetic resonance imaging (fMRI).

Some abilities within the visual system require many years of visual experience to achieve adult-like state. The perception of visual motion has been found to mature relatively late in comparison to other visual functions (Hollants-Gilhuijs, Ruijter et al. 1998; Schrauf, Wist et al. 1999; Gunn, Cory et al. 2002). The fact that perceptual skills mature at different rates has led to the suggestion that the development of the visual system occurs in discrete steps with different functions maturing at different times (Atkinson 2002). Different functions within the visual system are often associated with a concept of dividing the visual system into two functionally specialized streams (Milner and Goodale 1996). The ventral stream projects to the temporal lobe and is implicated in object and face recognition, while the dorsal stream projects to the parietal lobe and is involved in processing spatial information and visuomotor planning (Ungerleider and Mishkin 1982; Milner and Goodale 1996). It has been suggested previously that in normally developing children the course of development of the dorsal stream mechanisms may be more protracted than for the ventral stream. There is also strong evidence that the dorsal stream is more vulnerable to neurodevelopmental disorders ('dorsal stream vulnerability hypothesis') than the ventral stream, which has been described in children aged 4 years and older (Braddick, Atkinson et al. 2003).

Neuroimaging data provides evidence that processing of BM perception, the perception of other individuals' movements, confluences activity from the dorsal and the ventral stream brain areas with the posterior superior temporal sulcus (pSTS) representing a pivotal point within this network (Shiffrar 1994; Giese 2004). There is also evidence that in the perception of structure-from-motion both streams are involved (Murray, Olshausen et al. 2003).

Understanding the maturation of the dorsal and ventral stream, which are involved in structure-from-motion and biological motion perception in normally achieving children will help to define the neuronal basis for atypical perceptual and cognitive development in children.

# 2 Functional Magnetic Resonance Imaging (fMRI)

Functional magnetic resonance imaging (fMRI) is beside event-related EEG potentials (ERPs) the most widely used method for studying the neural basis of human cognition. fMRI provides us with a safe tool to study the interplay between brain and behavior. The fMRI method is non-invasive and, therefore, ideal for investigating children's brain function (picture of a MR-scanner see Figure 1).

fMRI is based upon the principles of nuclear magnetic resonance (NMR), a technique that is sensitive to the magnetic properties of molecules. The fMRI technique is capable to visualize the physiological changes in oxy- and deoxyhemoglobin concentration in cortical venous blood vessels, in particular the capillary bed, upon neuronal activation. The fMRI signal depends on the fact that there is closing coupling between changes in activity of a neuronal population and changes in its blood supply. Since fMRI can monitor focal changes in hemodynamic parameters, it provides only an indirect measure of neuronal activity.

The basic mechanism underlying fMRI is the blood oxygenation level-dependant (BOLD) contrast (Ogawa, Lee et al. 1990). Because the magnetic susceptibility of deoxyhemoglobin is greater than that of oxyhemoglobin, certain MRI measures are sensitive to changes in the ratio of deoxy- to oxyhemoglobin. The increase in blood supply triggered by increases in neural activity delivers more oxygen than is needed to meet metabolic demands. Therefore, the blood draining from an active neuronal population is more richly oxygenated than during the resting state. In consequence the ratio of deoxy- to oxyhemoglobin concentrations decreases, which leads to an increase in the MR signal.

Contrasting both active and resting states reveals areas of neuronal activation. Thus, fMRI is able to detect changes in neuronal activation between different states. The basic procedure to localize brain areas related to a specific function is to manipulate the experimental parameters over time and then examine where within the brain the hemodynamic signal changes specifically in relation to the experimental manipulation. As a result, an activation map is generated, showing which volume elements (voxels) in the brain correlate best with the changes in the experiment.

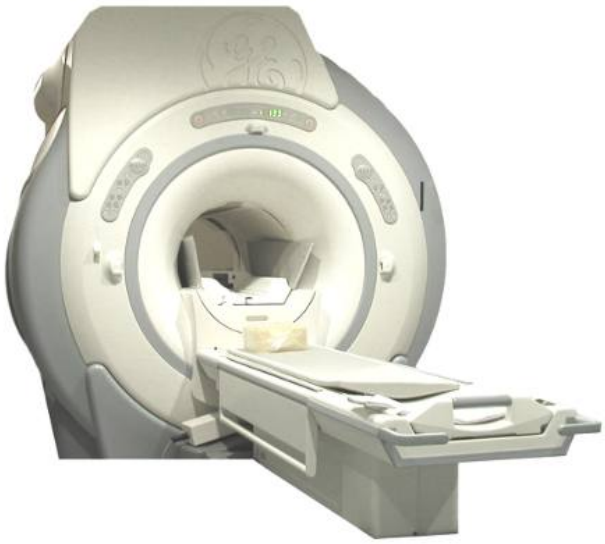

**Figure 1: A picture of a Signa 3.0 T (GE, Medical Systems) MR-scanner. The same scanner type was used for these investigations.**

## 2.1 Advantages and Disadvantages of fMRI Experiments

fMRI measurement has many advantages and a certain amount of limitations. It can non-invasively record brain signals (of humans or animals) without risks of radiation inherent in other scanning methods such as Positron Emission Tomography (PET) scans. Additionally, it can record on a spatial resolution in the region of 3-6 millimeters, but with relatively poor temporal resolution (in the order of seconds) compared with techniques such as EEG. However, this is mainly due to the phenomena being measured, not because of the technique. EEG measures electrical/neural activity while fMRI measures blood activity, which has a longer response. The MRI equipment used for fMRI can be used for high temporal resolution, if you measure different phenomena. In contrast to this it has to be mentioned that designs of fMRI experiments are quite restricted by the technical nature of the apparatus. As will be mentioned in the next chapter scanners are very noisy which makes it difficult to do auditory stimulation or investigate small children. Especially for small children it is also very difficult to remain motionless during a certain time. This means that only short experiments can be administered (probably max. 10 minutes). Furthermore, experiments have to be designed in a way to prevent subjects from moving, e.g. speech production can only be investigated by silent naming.

## 2.2 Functional Magnetic Resonance Imaging of Paediatric Populations

Many aspects of participating in an fMRI experiment can be challenging for preschool children (e.g., assessment in a medical environment, large and noisy equipment and confinement in a small space). Discomfort with the scanning procedure may affect performance and neural activation through decreased attention to instructions, decreased task performance and engagement of emotional and stress-related systems during the procedure. Explanation of, and acclimation to, the scanning environment prior to the actual fMRI data acquisition, is key to avoiding these problems.

### *2.2.1 Acclimation to the Imaging Environment*

It is particularly important to use a child-friendly approach even when the parents are first contacted in order to be asked to participate in the study. We decided to give children and parents an idea of how the scanning procedure is going to take place even before they decided to participate. In an attempt to ease reservation about the procedure and to alleviate anxiety we therefore attached a comic to the study information letter in which the scanning procedure was explained. The comic was based upon real pictures of the magnet room and all the persons being involved (child, parent(s), investigator, teddy bear) were drawn upon the pictures (see Figure 2).

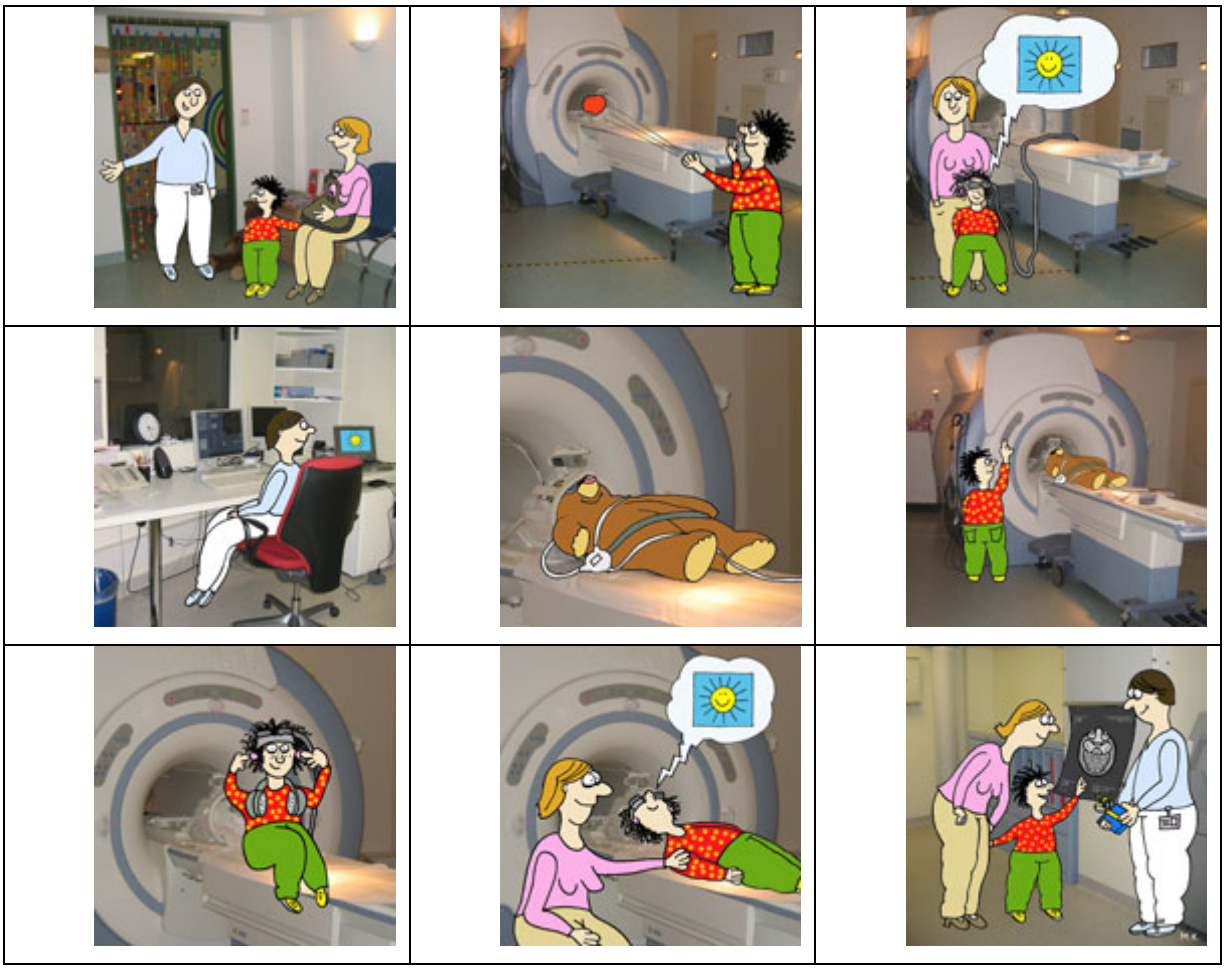

**Figure 2 :The comic being used in order to explain the scanning procedure to the child.**

Meeting with the child and guardian before the MRI, either on an earlier day or prior to scanning on the same day, may also help to alleviate anxiety about the procedure. Allowing the child to become familiar with the staff, to be trained on the task, and to gain experience with the scanner environment will increase the child's comfort and compliance. Minimizing the medical nature of this first appointment by the presence of hospital equipment, may also help to keep the anxiety level low for children or clinical populations who may have had prior negative medical experiences.

Simulation of the scanner experience allows the experimenter to acclimate the child to the future scanning procedure, assess the child's ability to remain still, and determine the child's ability to successfully complete a scan. This procedure can be achieved with presentation of pictures or a video of the scanner environment or through the child practicing at being still in a pretend magnet, while scanner sounds are played. Some sites have actual replicas of the scanner environment (‘mock

scanner') including bore, moving bed, and stimulus/response system in which they simulate the scanning procedure for participants. We decided not to use a so called 'mock scanner' since we think that children acclimate better if the real environment is being used instantly. When the child actually came to the investigation, a teddy bear was positioned on the scanner table. The procedure was explained to the child with the teddy bear serving as a dummy. The children could also act as investigators and move the teddy bear into the scanner.

### *2.2.2 Modifying the Scanning Environment for Pediatric Participants*

The actual scanner environment itself may present problems for children. For example, pediatric populations may differ in their perception and tolerance of loud sounds made by the scanner. While all subjects are required to wear some form of sound attenuation and hearing protection, additional efforts may improve the individual's comfort and performance, especially for patient populations sensitive to loud or unfamiliar noises. Standard ear protection, earplugs, will reduce the sound levels to below these distracting volumes. We additionally equipped the inside of the scanner with a sound diminishing foam mat.

A number of approaches can be used to make the scanner environment more child-

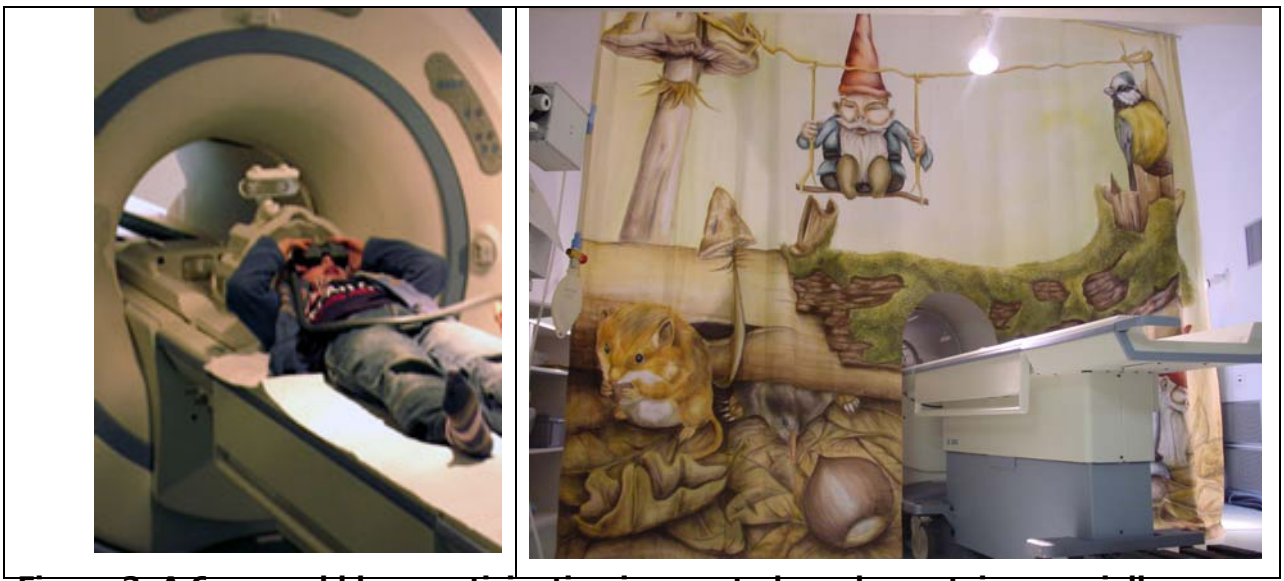

**Figure 3: A 6-year-old boy participating in our study and a curtain especially designed to make the children feeling more comfortable in the scanner environment and to minimize the medical nature of the equipment**

friendly. For example, showing the child a favorite video as they are moved into the bore of the magnet can reduce anticipatory anxiety. On the other hand wearing video goggles (see Figure 3) children do not actually realize that they are being

moved into a narrow pipe (this also helps slightly claustrophobic adult subjects). Once the child is comfortably placed in the scanner bore, there are a number of ways to decrease the children's anxiety during the data collection. First, to minimize boredom is to keep the child occupied, without interruption, through the experiment by showing a video through the structural and localization scans. Second, the sense of isolation – the child is usually alone in the magnet room - can be decreased by having the experimenter or parent interact with the child between runs using an interphone system. Alternatively, in cases where the child is particularly anxious, the parent may be pre-screened for metal, given ear protection, and allowed to stay in the scanning room with the child.

# 3 Visual Motion Perception

Within a human brain, numerous neural regions located throughout the central nervous system exhibit enhanced activity in response to the presentation of a moving visual stimulus. From this selectivity for moving visual stimuli arises the ability to perceive motion based solely on visual sensory input.

The functional significance of visual motion perception cannot be overstated. The visual motion perception allows humans to establish the 3-D structure of a visual scene and allows for the organization of retinal image features into the objects actually present in the visual scene (image segmentation). Analysis of visual motion also aids in guiding balance and posture, as well as estimating the direction of the observer's own path of motion and time to collision with objects and surfaces in the surroundings. One of the most obvious and important functions of visual motion perception is to encode and represent the trajectories of moving real-world objects in order to enable a behavioral response to those movements.

In the real world target objects are often moving or the subject herself/himself is moving. The human (and of other vertebrates') visual system therefore is selective for two broad categories of visual motion: the motion of objects in the visual array (such as predators and prey) and self-motion relative to the environment. As organisms move through an environment containing numerous stationary visual stimuli distinct and informative flow fields, or optic flow, occurs across the entire retina. The analysis of optic flow provides information required to stabilize the retina and head during object viewing, to maintain the human's posture, and to estimate the human's motion through space (including navigation and distance estimation). Most optic flow information is processed by a discrete visual pathway called the accessory optic system (AOS).

The analysis of self-motion is fundamentally different than the analysis of object motion. The analysis of object motion, or animate motion, relies on neural mechanisms which have double-opponent, directionally selective, and center-surround receptive fields that respond to motion in the preferred direction in the center of the receptive field but are inhibited when the same direction of motion occurs in the large surround of the receptive field. Thus, the motion of small objects in the preferred direction will excite these neurons. Conversely large patterns of optic flow, such as those generated by an animal's own motion, will not excite these neurons because the center and surround of the receptive field oppose each other.

Indeed, neurons in the AOS have large single-opponent receptive fields that are better suited to respond to optic flow stimuli.

## 3.1 The Dorsal and Ventral Visual Pathways and their Role in Structure-from-motion and Biological Motion Processing

The visual system forms representations of many properties of the environment including information about the shapes of objects and their motion. Shape and motion are features with seemingly complementary properties. Inferring object shape involves detecting spatial relationships among features whereas object motion detection involves solving a temporal problem. The complementary quality of shape and motion appears to be reflected in the organization of the visual system (Ungerleider and Mishkin 1982). In the human visual system, certain cortical areas, such as area hMT+, appear to be specialized for motion processing (Zeki, Watson et al. 1991; Sunaert, Van Hecke et al. 1999) and the lateral occipital complex (LOC) area seems to be important for object shape processing. Visual information processing is therefore divided into two relatively separate streams in the brain. The detailed connectivity of these cortical routes is very complex, but, in simplified terms, one pathway (the ventral route) extends form the primary visual cortex through parts of the temporal lobe, while the other pathway (the dorsal route) goes from the primary visual cortex to the parietal cortex. The exact point at which the routes separate is still debated.

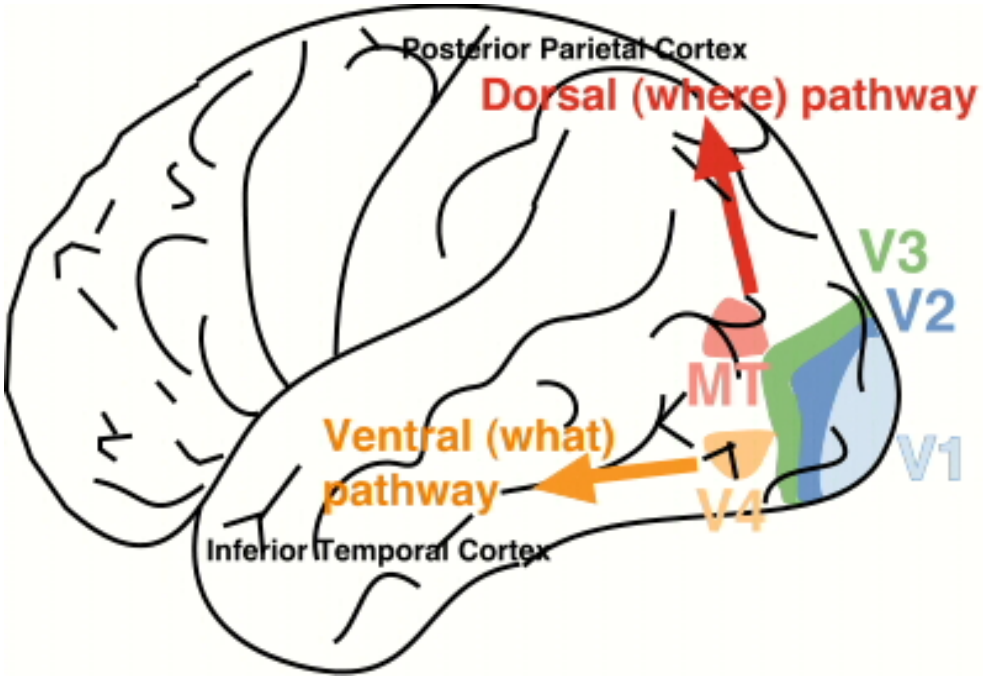


**Figure 4: Distinct visual areas within the human dorsal and ventral pathway**

The dorsal stream, sometimes called the "Where Pathway", is associated with motion, representation of object locations, and control of the eyes and arms, especially when visual information is used to guide saccades or reaching (see Figure 3). From animal studies it is known that cells within the dorsal pathway have small receptive fields and some continue to respond after the stimulus has disappeared (Newsome, Wurtz et al. 1988) suggesting that these cells are involved in tracking of moving objects.

The ventral stream, sometimes called the "What Pathway", is associated with form recognition and object representation (see Figure 3). It is also associated with storage of long-term memory. The properties of neurons in the adult ventral stream seem complementary to those in the dorsal stream. As one proceeds along the ventral stream, cells respond to more and more complex clusters of features. At the higher levels, the complex cells show remarkable selectivity in their firing. Many of the cells have very large receptive fields on the retina. That means that although they can process feature information, they lose much of their spatial resolution on the retina.

There is a close link between the two features of object and motion. Motion can be an important cue for recognizing object boundaries and tracking shape features over time is the basis of motion computation. Shape-from-motion perception or in other words, structure-from-motion perception is the perception of three-dimensional shape from motion cues. Indeed, SFM stimuli demonstrate that motion information alone can create vivid 3-D shape perceptions (Wallach and O'Connell 1953; Braddick 1974). A special type of SFM perception is BM perception - the perception of other individual actions from only very reduced displays. BM perception is an important cue in every day human social interaction. When human beings communicate with each other, speech and audition are dominant, with visual perception of gestures, eye contact, and expressions playing a strong supporting role. The extrastriate area most closely associated with BM perception is the posterior superior temporal sulcus (pSTS) (Grezes, Fonlupt et al. 2001; Vaina, Solomon et al. 2001; Grossman and Blake 2002) and represents a pivotal point within the dorsal and the ventral stream. There is evidence from clinical studies that the perception of human motion but not the perception of continuous motion can be disrupted if damage occurs in pSTS (Vaina and Gross 2004).

The final pathway, the Accessory Optic System, is a subcortical pathway and as mentioned in the previous chapter, necessary for the perception of self-motion and gaze stabilization.

## 3.2 Development of Ventral and Dorsal Pathways

Determining the age at which various aspects of visual processing mature is important for understanding the development of the visual system and for studying childhood clinical populations. Clinical diagnosis and research often focus on measures of acuity. However, acuity taps only part of the broad spectrum of tasks that we use vision to accomplish. For example, motion processing ability, which is not correlated with acuity, is crucial for tasks such as visually guided locomotion, crossing a busy street, catching and throwing, etc. Pediatric clinical populations with motion perception deficits include: dyslexia (Cornelissen, Richardson et al. 1995; Demb, Boynton et al. 1998; Edwards, Giaschi et al. 2004), amblyopia (Giaschi, Regan et al. 1992; Simmers, Ledgeway et al. 2003), autism and (Milne, Swettenham et al. 2002) mental retardation (Fox and Oross 1990).

The main findings from behavioral and electrophysiological studies on the relative development of form and motion processing mechanisms that can be thought of as functions of the ventral and dorsal cortical streams, respectively are summarized in Figure 4.

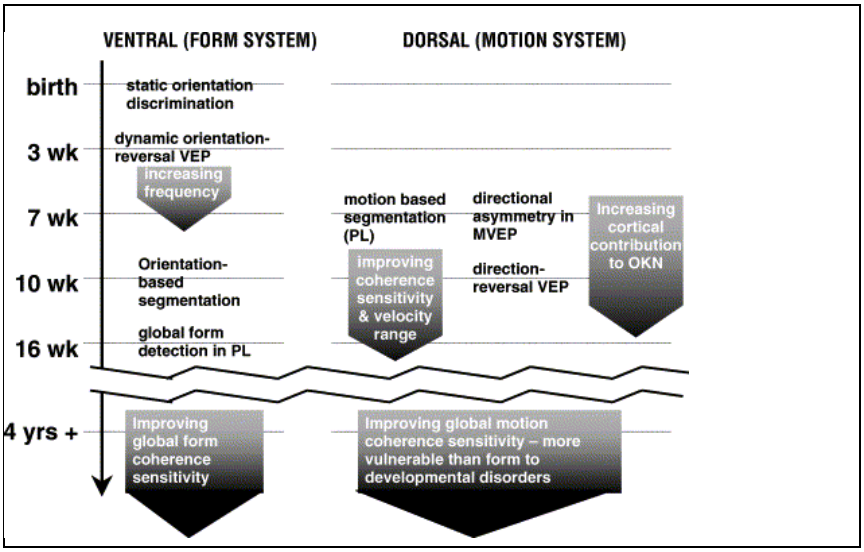


**Figure 5: Main findings from behavioral and electrophysiological studies on the relative development of form and motion processing (Figure used with permission from (Braddick, Atkinson et al. 2003).**

## 3.3 Development of Biological Motion and Structure-from-Motion Perception

Sensitivity to BM stimuli is considered to occur very early in perceptual development (see (Pinto 2005) for review). Experiments of BM perception in infants revealed that 4-moth-olds prefer an upright walker to the same pattern turned upside-down (Fox and McDaniel 1982). At 3-5-months of age (Bertenthal, Proffitt et al. 1987; Bertenthal and Pinto 1994) but not in 2-month-old infants (Fox and McDaniel 1982) a visual preference for BM is found. However, these results only propose that infants - like adults - are sensitive to stimulus manipulations that affect the quality of BM portrayed by point-light figures (see (Bertenthal, Proffitt et al. 1984) for discussion). These findings only indicate that infants prefer BM but they do not imply that they understand point-light sequences as depicting human movements. Beyond infancy there are only a few comparisons of sensitivity to BM of typically developing children and adults. In studies including young children, they generally served as an age matched control group for the comparison to a clinical population such as autistic children (Blake, Turner et al. 2003), children suffering from Williams Syndrome (Jordan, Reiss et al. 2002) or adolescents with motor impairments associated with periventricular leukomalacia (PVL) (Pavlova, Staudt et al. 2003). There are only a few studies that provide evidence on the sensitivity of typically developing children to BM.

Pavlova et al. (Pavlova, Krageloh-Mann et al. 2001) found that 3-year-olds were able to recognize a walking person in a point-light display but performance linearly increased with age up to the age of five. Likewise, no correlation between age and accuracy of performance could be detected in a study of typically developing 5- to 10-year-old children (Blake, Turner et al. 2003). Most probably ceiling levels were reached early in these studies. Thus, differences in sensitivity to BM have been observed between children over 5 years of age and adults only when point-light animations were embedded within an array of dynamic noise dots (Jordan, Reiss et al. 2002; Blake, Turner et al. 2003; Freire, Lewis et al. 2006) – which has previously been used to make the recognition of BM more demanding (even though not impossible) (Bertenthal and Pinto 1994; Pavlova, Krageloh-Mann et al. 2001; Ikeda, Blake et al. 2005).

The detection of structures-from-motion (SFM) at least partly depends on the detection of coherent motion. At some stage, however, shape processing needs to be activated by coherent motion. Braddick and colleagues (2003) suggested that

the development of integrative processing in SFM is constrained by the development of global coherent motion processing. This idea was based on findings that perception of BM or SFM develops at about the same age as the detection of coherent motion. For example, 3-6-month-old infants can already detect SFM (Kaufmann-Hayoz, Kaufmann et al. 1986; Yonas, Arterberry et al. 1987; Arterberry and Yonas 1988; Arterberry and Yonas 2000) but reach a mature level at the age of 7 (Parrish, Giaschi et al. 2005).

# 4 Developmental Brain Plasticity

In recent years, neuroimaging techniques have shown that developmental changes of the human brain occur from infancy through adolescence (see (Paus 2005) for review). These developmental changes are based on maturation and neuroplasticity, which refers to the lifelong ability of the brain to reorganize neural circuits based on experiences or sensory stimulation. Plasticity is the mechanism for emerging competencies and skill acquisition, and allows the brain to adapt itself to its environment. In order to learn and improve new skills, there must be persistent functional changes in the brain that represent new abilities (Elbert, Heim et al. 2001). Brain plastic changes occur at multiple levels of neuronal organization, from molecules and synapses to cortical maps and neural networks (Buonomano and Merzenich 1998). The brain mechanisms underlying plasticity are based on adjustments in the strength of connections between brain cells, reflected by alterations in the internal structure and number of synapses.

Early brain development is characterized by rapid brain growth (Garey 1984). The proliferation and overproduction of neurons occurs prenatally, whereas cell death (apoptosis) begins prenatally and continues until the second postnatal year. Likewise, an overproduction of cell arborization and synaptic contacts can be observed in the first years of life, which then is followed by an elimination of 'pruning' phase (Huttenlocher, de Courten et al. 1982; Huttenlocher and de Courten 1987; Huttenlocher 1990). Synaptic pruning eliminates weaker synaptic contacts while stronger connections are kept and strengthened. Experience, as a result of exposure or training , determines which connections will be strengthened and which will be pruned. Connections that have been activated most frequently are preserved, a mechanism referred to as Hebbian competition (Hebb 1949). The importance of postnatal experience for the normal development of the visual system has been proven by lid suture of one eye in kittens (Hubel and Wiesel 1962). Similarly, abnormal visual development was observed in children born with bilateral or unilateral cataracts (Lewis and Maurer 2005; Maurer, Lewis et al. 2005). This opacity in the lens allows only diffuse light to reach the retina, and expressed by pattern deprivation in the affected eye. The final outcome of visual acuity and other visual functions depends on the onset and duration of the cataract, which can be removed by surgical intervention.

Maturational changes are also present in the white matter structure. Accordingly, myelination has been found to undergo mainly linear progressive changes throughout childhood and adolescence, as evidenced by both anatomical studies (Conel 1939-1967; Yakovlev and Lecours 1967) and morphometric MR imaging (Giedd, Blumenthal et al. 1999; Paus, Collins et al. 2001). The increase in white matter with age has been interpreted as reflecting increased axonal myelination in the frontal and parietal cortices during this time period.

While the increase in white matter in certain brain regions seems to be linear across all brain areas, changes in grey matter density appear to follow a region-specific, non-linear pattern. Rather than a simple linear change in grey matter with age, studies suggest a perturbation in grey matter density development that more or less coincides with the onset of puberty. The grey matter changes may reflect the synaptic reorganization that occurs at the onset of and after puberty (Huttenlocher 1979). Thus, the increase in grey matter apparent at the onset of puberty (Giedd, Blumenthal et al. 1999) might reflect a wave of synapse proliferation at this time. The gradual decrease in grey matter density that occurs after puberty in certain brain regions has been attributed to post-pubescent synaptic pruning (Giedd, Blumenthal et al. 1999; Sowell, Trauner et al. 2002; Gogtay, Giedd et al. 2004).

In sum, brain development can be described by the emergence of new networks and refinement of connections, which allow information processing to get faster and more efficient. Thus, functional brain plasticity involves both temporal and spatial reorganization of neural circuits, which can be investigated with ERP and fMRI respectively. Spatial reorganization is best reflected by changes in the fMRI activation pattern, expressed by increases or decreases of activity in particular brain regions, changes in hemispheric lateralization or a progressions from more diffuse to more focal activation pattern (Casey, Tottenham et al. 2005).

# 5 Conclusions & Hypotheses

The development of visual functions is relevant for the overall cognitive development in childhood. Much behavioral work has been done investigating the development of vision in infants and children. However, little is known about the changes in the underlying neuronal networks. Findings from developmental neuroimaging studies are conflictive. Some studies provide evidence that the spatial organization of the visual network gets established early in childhood (Conner, Sharma et al. 2004) and others have found contradictory results (Passarotti, Paul et al. 2003; Passarotti, Smith et al. 2007). As far as we know there is no other functional imaging study investigating dorsal and ventral stream development in children age 5-7.

The main goal of this thesis is to clarify the functional reorganization of visual areas associated with structure-from-motion and biological motion perception during child development. We sought to examine which plastic changes in distribution occur in the neuronal network for processing these two types of motion perception.

The visual system depends extensively on postnatal experience in order to develop and reach adult-like state (Maurer, Lewis et al. 2005). The maturation of dynamic form processing has been found to mature late and does not reach adult levels before the age of 15 years (Ishigaki and Miyao 1994; Schrauf, Wist et al. 1999). Furthermore, the development of visual motion processing has been found to be relatively protracted to the development of static form perception (Hollants-Gilhuijs, Ruijter et al. 1998; Hollants-Gilhuijs, Ruijter et al. 1998; Schrauf, Wist et al. 1999; Gunn, Cory et al. 2002). Because slowly developing systems such as the dorsal stream (‘dorsal stream vulnerability hypothesis’) have been proposed to be more plastic and vulnerable (Atkinson 2000; Braddick, Atkinson et al. 2003), it is of high relevance to understand these late maturational changes.

Whilst the first study describes the development of the neuronal correlates of SFM perception, the second focuses on developmental aspects of BM perception. Both studies compare adult data with results obtained in preschool and school age children. In the SFM experiment (mean age range 5y 6m – 6y 9m) the children were in average one year younger than in the BM perception experiment (mean age range 5y 2m - 7y 2m). The first study was a perceptual task whereas in the second

study the subjects had to indicate what they saw. Both experiments were designed to explore the development of extrastriate areas involved in the corresponding visual motion task. In both studies the emphasis was laid upon dorsal and ventral stream development as the processing of both tasks involve areas within those two streams. The main question was how the neural structures seemingly involved in SFM and BM processing develop and how, at least in the BM experiment, the development of these structures is correlated with behavioral performance. Specifically for the structure-from-motion experiment, we also hypothized whether age related differences only occur in stimuli that require high order visual processing. In the BM perception task it is known that in preschool children performance decreases if the stimuli are presented within an array of randomly moving dots (noise) (Freire, Lewis et al. 2006). We therefore additionally included such a condition. It is known that in adults masking visual stimuli affects the neural activity within task-specific areas (Grossman, Blake et al. 2004). For this condition we therefore asked whether and how neural activity in task-specific areas would be affected in adults as well as in children. Furthermore it is known that in children, task-unspecific activation decreases and task-specific activation increases with development (Booth, Burman et al. 2001; Casey, Casey et al. 2002). We therefore expect them to show additional task-unspecific activity within fronto-parietal areas regions.

# 6 Dorsal stream development in motion and structure-from-motion perception[1]

**Klaver P, Lichtensteiger J, Bucher K, Dietrich T, Loenneker T, Martin E.**

## 6.1 Abstract

Little is known about the neural development underlying high order visual perception. For example, in detection of structures by coherently moving dots, motion information must interact with shape-based information to enable the recognition objects. Tasks involving these different motion-based discriminations are known to activate distinct specialized brain areas in adults. Here, we investigate neural development of normal developing children using functional magnetic resonance imaging (fMRI) during perception of randomly moving point-light dots (RM), coherently moving dots that formed a 3D rotating object (SFM), and static dots. Perception of RM enhanced neural activity as compared with static dots in motion processing related visual areas, including visual area 3a (V3a), and middle temporal area (hMT+) in ten adults (age 20-30 years). Children (age 5-6 years) showed less pronounced activity in area V3a than in adults. Perception of SFM induced enhanced neural activity as compared to RM in adults in the left parietal shape area (PSA), whereas children increased neural activity within dorsal (V3a) and ventral brain areas (lingual gyrus) of the occipital cortex. These findings provide evidence of neural development within the dorsal pathway. First, maturation was associated with enhanced activity in specialized areas within the dorsal pathway during RM perception (V3a) and SFM perception (PSA). Secondly, high order visual perception related neural development was associated with a shift in neural activity from low level shape and motion specialized areas in children, including partially immature area V3a, to high order areas in the parietal lobule (PSA) in adults.

[1] article in NeuroImage, In Press, Corrected Proof, Available online 22 November 2007

## 6.2 Introduction

Research on visual perception and cognition has led to the understanding that vision is not merely a matter of passive perception; but rather an intelligent process of construction ((Zeki 2001) and references therein). These constructive processes are age-dependent and reflect the integration of colour, shape and motion information into the representation of the child's environment. A neurobiological theory of visual development postulates at least three visual systems: one early, rudimentary subcortical and two cortical systems (Atkinson 1984; Atkinson 2000). One cortical system comprises areas located in the ventral occipital and temporal lobes. It is commonly referred to as the "what" pathway because damage to these regions leads to deficits in the ability to discriminate between visual objects. The other cortical system includes areas located in the dorsal occipital and parietal lobes. It is commonly referred to as the "where" pathway because damage to these regions leads to deficits in the ability to identify the locations of visual objects in space (Ungerleider and Mishkin 1982; Haxby, Grady et al. 1991; Milner and Goodale 1995). Whereas the ventral pathway is prone to process, among others, visual identity and feature information (e.g. colour, luminance, faces and object identities), the dorsal pathway is inclined to process spatial relations and motion direction information.

There is strong evidence that the dorsal stream is more vulnerable to neurodevelopmental disorders than the ventral stream, which has been described in children aged 4 years and older (Braddick, Atkinson et al. 2003). In normally developing children the parsing of the visual array into globally organized forms appears to develop more securely than the equivalent parsing by relative motion. The integration of local motion into the perception of coherent translational global motion is a basic integrative process of the motion pathway, for which norms of behavioural performance in the 4-10 year age range are already established (Gunn, Cory et al. 2002; Parrish, Giaschi et al. 2005). Recent findings, however, animated the unresolved debate on the neural mechanisms underlying the development of motion processing, particularly after four years of age. For example, a recent functional brain imaging study showed that full development of coherent motion in hMT+ is not reached until adolescence (Bucher, Dietrich et al. 2006). Tasks

inducing dynamic visual adaptation (Schrauf, Wist et al. 1999), configural object recognition (Rentschler, Jüttner et al. 2004) and haptic priming upon configural visual stimuli (Jüttner, Müller et al. 2006) require even stronger visual processing demands and possibly the involvement of dorsal stream processing in object recognition. It has been shown that these functions do not mature until adolescence.

The detection of structures-from-motion (SFM) at least partly depends on the detection of coherent motion. At some stage, however, shape processing needs to be activated by coherent motion. Braddick and colleagues (2003) suggested that the development of integrative processing in structure from motion is constrained by the development of global coherent motion processing. This idea was based on findings that perception of biological motion or structure from motion develops at about the same age as the detection of coherent motion. For example, 3-6-month-old infants can already detect SFM (Kaufmann-Hayoz, Kaufmann et al. 1986; Yonas, Arterberry et al. 1987; Arterberry and Yonas 1988; Arterberry and Yonas 2000). Others, however, suggested that a third area, probably in the posterior, superior parietal cortex, needs to be activated that binds both motion and shape processing areas (Zeki 2001). This (temporary) binding between shape and motion may be related to attention or spatial processing, and which may have a different developmental time course (Ross-Sheehy, Oakes et al. 2003; Rentschler, Jüttner et al. 2004; Oakes, Ross-Sheehy et al. 2006). Thus, it remains unknown to what extend neural development of SFM processing depends on both the development of motion processing related areas and areas that are not directly related to shape or motion processing.

Brain imaging studies in adults showed that random motion (RM) activates areas at different levels of the cortical motion pathways, including dorsal visual area 3a (V3a), area V5 (middle temporal area hMT+), the inferior/superior parietal lobule and ventral areas in the lingual and fusiform gyrus (Cornette, Dupont et al. 1998; Sunaert, Van Hecke et al. 1999). In contrast to RM, coherent motion activates areas in the parietooccipital junction, but also enhances activity in extrastriate areas responding to RM (Braddick, O'Brien et al. 2000; Braddick, O'Brien et al. 2001). As compared to RM, 3D SFM also activates areas within the parietooccipital cortex and parietal cortex, but some studies also reported enhanced activity in extrastriate areas related to RM perception (Orban, Sunaert et al. 1999; Paradis, Cornilleau-Peres et al. 2000; Murray, Olshausen et al. 2003). The question

is whether young children up to the school age show differences in brain activity during RM perception, and whether these differences are limited to the certain parts of the dorsal stream. A further question is whether the limitations observed in high order visual capacities of 5-6 year old children are associated with high order visual areas and functions. In this case one may hypothesize that age related differences only occur in stimuli that require high order visual processing. Alternatively, age related differences may be due to maturation in low order visual processing areas, in which case stimuli requiring both low and high order visual processing would induce age related differences in neural activity. Here, we measured neural activity in adults and 5-6 year old children in an fMRI experiment while they perceived RM stimuli and SFM stimuli. Because of limitations in scanning time in young children we did not include an intermediate coherent motion condition. We found that adults activated dorsal and ventral occipital areas during RM perception in contrast to perception of static dots and that children showed less pronounced activity in dorsal area V3a. High order perception of SFM stimuli enhanced neural activity in adult parietal cortex as compared with RM. Children showed less pronounced activity in this area, but more in lower visual areas related to shape and motion processing.

## 6.3 Methods

### *6.3.1 Subjects*

Ten normal achieving pre-school children (mean age 6 years, range 5 y 6 m – 6 y 9 m, 4 male) and ten right handed adults (mean age 26 years, range 20-29, 4 male) were scanned. All subjects and parents of the children gave written informed consent prior to participation. All subjects had no history of neurological or psychiatric disorder. The children were slowly introduced to the scanner and its equipment. For all children, a teddy bear was positioned on the scanner table in order to explain the scanning procedure to the child in an attempt to ease reservations about the procedure an alleviate anxiety. Children were able to watch a cartoon video during anatomical acquisitions. In order to improve compliance and reduce head motion, children listened to a story presented on the headphone. Because of a limitation in head space within the MR head coils we chose to not use a headphone in adults. Parents stayed outside the scanner room but were able to

talk to the children between the scans. The study was approved by a local ethics committee. The families were given a child's story-CD as a token of our appreciation. Adult volunteers were given financial compensation for their participation.

### *6.3.2 Stimuli*

Subjects viewed randomly moving dots (RM), moving dots that formed a 3-D rotating structure by coherent movement (SFM) and static dots (STAT) as control stimuli. The stimuli were downloaded from the reference provided by Murray and colleagues (http://redwood.uncdavis.edu/scott/research/sfm/; see Figure 5a for a schematic illustration, adapted from Murray et al. 2003). All stimuli consisted of an array of 450 dots subtending 10° of visual angle. For RM stimuli each dot moved in a random direction with constant speed (4°/s). The dots in the SFM condition were projections of rigid, transparent, geometric shapes including a cube, cylinder and 'house shaped' figures. Dots were randomly selected from a uniform distribution on the object surface and kept fixed relative to the rotating object surface and orthographically projected onto the image plane. Dots were rotated on a randomly chosen 3-D axis for 40° in 1.5° increments. Both motion stimuli had the same direction and speed, but direction and speed were randomly reassigned to different dots to create random motion. The motion stimuli were generated by creating moving sequences at a rate of 20 Hz with 28 frames stored as a bitmap. A sequence of 80 frames was played forward and backward so that motion was continually observed. The first frame was the same for every SFM and RM. The baseline (STAT) presented the 25th frame from the RM stimuli. The total presentation time of each stimulus was 4000 ms. Stimuli were presented through optical goggles during a 12 minute scanning session. The three conditions were presented in a balanced order of 18 blocks of trials that were separated by a 2 second interval (54 trials per condition, 4 seconds per trial). All subjects were instructed to passively view the stimulation.

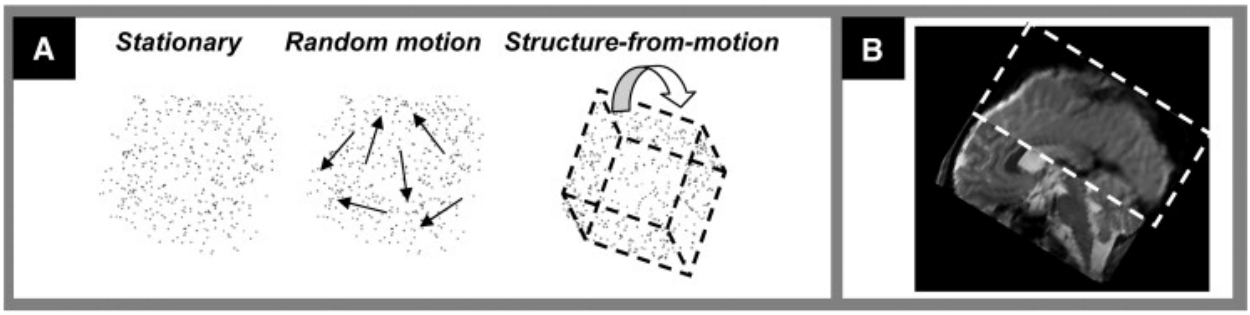


**Figure 6: (A) Three types of stimuli were presented, static dots, randomly moving dots and moving dots that formed 3D structure (cylinder, box or 'house shaped' figures. These stimuli were adapted from Murray et al. (2003). (B) AN example of partial functional brain imaging perpendicular to the V1 coronal axis, thus covering the occipital cortex and parietal lobule.**

### *6.3.3 fRMI data acquisition and analysis*

Brain images were acquired on a 3.0 T Scanner (General Electric, Milwaukee USA) using a standard 8-channel head coil. To estimate blood oxygenation level dependent (BOLD) contrast 343 echo planar imaging (EPI) scans were acquired including 2 dummy scans. The scans were aligned perpendicular to the V1 coronal axis thus covering the occipital and parietal lobe (see Figure 5b for an example). Scan parameters were: number of slices (NS): 26; slice thickness (ST): 2.7 mm; matrix size (MS): 96×96 zero-filled to 128×128; field of view (FOV): 230 mm; flip angle (FA): 50°; echo time (TE): 32 ms; repetition time (TR): 2 s. The task was presented via video goggles (MRI Audio/Video System, Resonance Technology, Inc., USA) using Presentation software (www.neurobs.com). Additionally, a high-resolution anatomical reference T2-weighted scan was acquired (NS: 52; ST: 2.7 mm; MS: 256×256; FOV: 230 mm; FA: 90°; TE: 12.3 ms; TR: 10.6 s). Functional MRI data analysis was done using Statistical Parametric Mapping 2 (SPM2, www.fil.ion.ucl.ac.uk/spm/). Pre-processing included realignment with unwarping. No subject was excluded from the analysis because of excessive movement, since only one child had maximum movement of 3.5 mm in z-direction. All other subjects did not exceed 2.5 mm movement in z-direction and 1.5 mm in all other directions, which was less than 1 voxel size. We transferred functional and anatomical data from adults and children into a common stereotactic space. For this purpose, T2 images of all subjects were segmented, and normalization parameters were estimated for grey matter images on a standard grey matter template in Montreal Normalization Institute space. The EPI images data were coregistered upon the T2 image and normalization parameters were applied to both the T2 images (1 $mm^3$)

and EPI images (3 $mm^3$). EPI data were then smoothed with a 6 mm full width at half maximum Gaussian kernel. The hemodynamic response was modelled by a stick function to each stimulus presentation in each category convolved with a canonical hemodynamic response function and its temporal derivative. Parameter images were generated for each adult and child for the contrasts STAT, RM and SFM. We applied two-sample t-tests in a second level random-effect analysis for the contrasts RM-STAT and SFM-RM. Significant voxels are reported ($p<0.001$, uncorrected) within clusters of 20 voxels, which was the threshold of a significant cluster after correction for multiple comparisons ($p<0.05$). We further performed a region of interest (ROI) analysis on signal changes from voxels within 10 mm spheres around mean local maxima in the left and right hemisphere reported by Murray and colleagues (2003). These ROIs were related to motion processing (LOS left x = -27/y= -91/z = 8, right 34/-88/4; V3a left -19/-91/24, right 21/-90/22; hMT+ left -45/-73/5, right 48/-66/2), shape (LO left -39/-82/-2, right 41/-81/2, SLO left -33/-82/15, right 37/-78/12, PF left -43/-70/-7, right 45/-65/-8) and structure-from-motion processing (parietal shape area, PSA left -34/-49/58, right 35/-47/59). For contrasts RM-STAT and SFM-RM ANOVAs were performed on the within-subject factors stimulus, ROI (7), hemisphere (left, right) and between-subject factor group (adult, child).

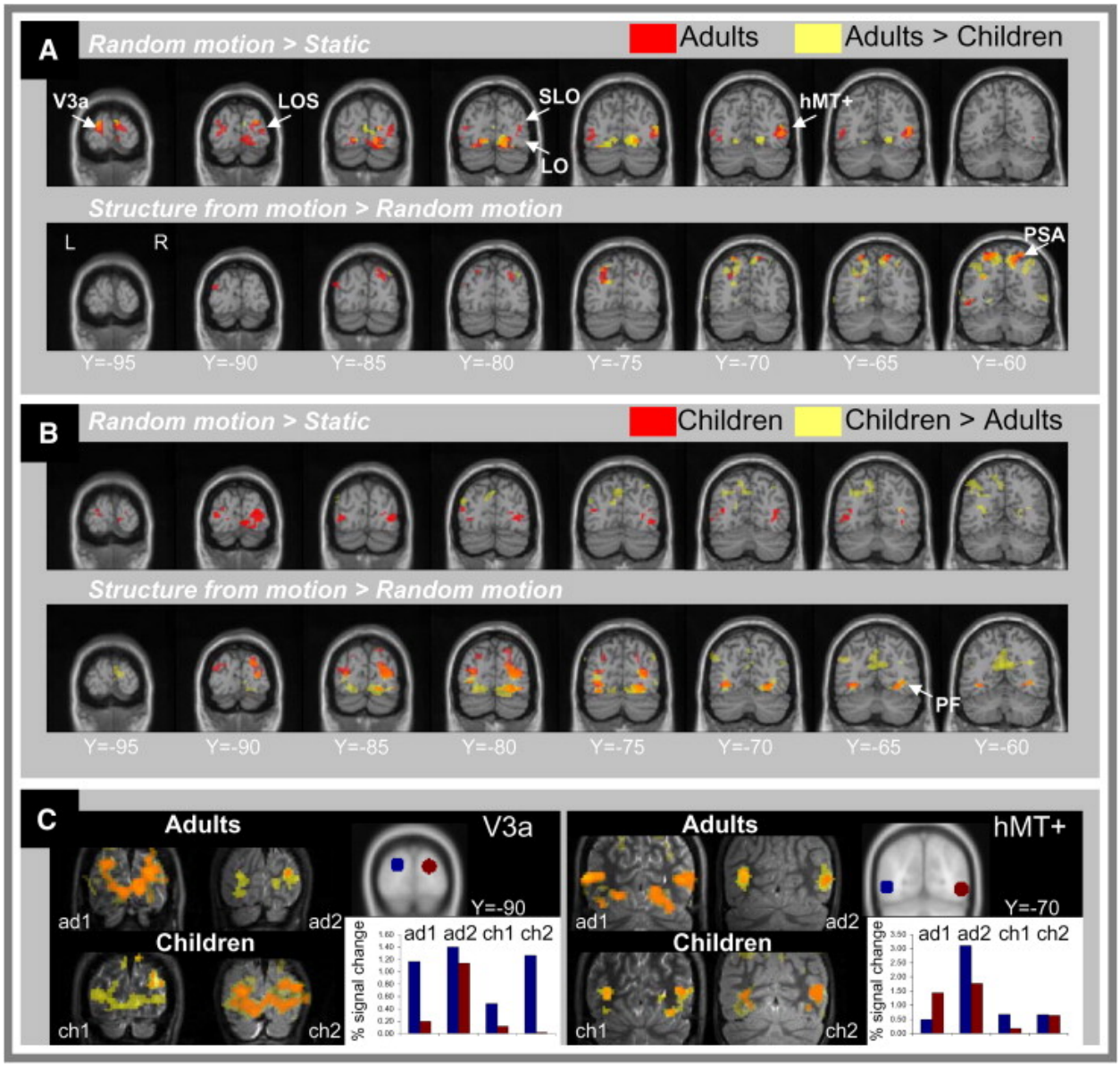


**Figure 7: (A) Statistical maps overlaid on coronal slices of a canonical structural MR image. Displayed are the within-subject contrasts for adults (red, $p < 0.001$) and between-subject contrasts (yellow, adults>children, $p<0.05$) for random motion>static (top), structure-from-motion>static (center) and structure-from-motion>random motion (bottom). (B) Same as A, but for within-subject contrasts in children and between-subject contrasts (children>adults). (C) Two exemplar adults (ad1/ad2) and children (ch1/ch2) are displayed at two statistical thresholds (yellow, $p<0.001$ uncorrected, orange $p<0.05$ corrected the whole brain). The left side shows left (dark blue) and right (dark red) area V3a ($y=-90$) and percent signal change within these ROIs. The right side shows the same for the left and right area hMT+ ($y=-70$). It shows that adults and children both show significant neural activity in areas V3a and hMT+, but with different levels of neural response. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)**

It is not trivial to generalize ROIs from adult subjects to children, because the location of specialized brain areas may be shifted within the developing brain. Previous studies have tested the possibility to generalize across age within a common space for 7 year old children (Burgund, Kang et al. 2002; Kang, Burgund et al. 2002). The children were one (maximally 2) years younger than in the study by Kang and colleagues, which was considered to be a similar age group. In order to verify the normalization procedure and the choice of ROIs the contrast between RM and STAT was calculated in two exemplary subjects at two significance levels ($p<0.05$ corrected for the whole brain and $p<0.001$ uncorrected). Percent signal changes were also calculated from two ROIs (areas V3a and hMT+). It could be shown (Figure 6C) that similar clusters were activated by RM in adults and children, but that the level of activity was different, particularly in area V3a. This result justifies the choice of ROIs and do not suggests that brain areas are shifted with age in this sample.

## 6.4 Imaging results

### *6.4.1 Motion*

Figures 6A and 6B show fMRI results from adults and children. As compared with static stimuli RM yielded enhanced neural activity in adults in the lateral and dorsal part of the occipital cortex, as well as in the ventral occipital cortex and posterior middle temporal gyrus (Figure 6A). These areas correspond to previously described bilateral lateral occipital sulcus (LOS), visual area 3a (V3a) and middle temporal area (hMT+) (Tootell, Mendola et al. 1997; Orban, Sunaert et al. 1999; Sunaert, Van Hecke et al. 1999; Murray, Olshausen et al. 2003). A similar pattern of brain activity was found in children (Figure 6B), with few apparent differences in the distribution. Children showed enhanced activity in bilateral LOS, but less in medial occipital areas that extend into dorsal and ventral parts of the occipital cortex (see Table 1 for detailed results) and in hMT+. Whole head analysis showed no significant differences between groups except for a larger effect for RM in children than adults in the left precentral gyrus (Talairach coordinates $x = -36$, $y = -15$, $z = 45$, $Z = 4.2$, $p<0.001$).

The ROI analysis (collapsed over left and right hemisphere, Figure 7A, top part) showed differences in the neural response to RM in different regions (ROI: $F_{6,108}$= 11.0, p<0.001). Significantly enhanced activity was found in adults and children in motion processing related areas (LOS, V3a, hMT+, all p<0.001) as well as in shape related areas lateral occipital (LO), superior lateral occipital (SLO) and posterior fusiform (PF) (all p<0.001), but not in SFM related area parietal shape area (PSA). A significant interaction between group and ROI ($F_{6,108}$= 4.5, p=0.004) indicated that RM induced larger neural activity in adults than in children in motion sensitive area V3a (adult > child $t_{18}$ = 2.9, p < 0.01). A trend to significance was found in hMT+ ($t_{18}$ = 1.8, p < 0.09). Further, there was a significant hemispheric lateralization effect in LO that did not depend on maturation (right > left LO, p < 0.01).

Table 1: Significant statistical comparisons are shown for random motion and structure from motion in children and adults

| **Effect** | **Area** | **BA** | **Coordinates LH** | | | ***Z*** | ***p*-value** | **Coordinates RH** | | | ***Z*** | **p-value** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | ***x*** | ***y*** | ***z*** | | | ***x*** | ***y*** | ***z*** | | |
| *Adults* | | | | | | | | | | | | |
| Random > Static | Middle occipital g. | 18/19 | − 18 | − 92 | 16 | 5.1 | 0.003 | 21 | − 93 | 13 | 4.3 | 0.006 |
| | Middle temporal g. | 19/39 | − 42 | − 70 | − 2 | 4.0 | 0.01 | 45 | − 70 | 6 | 5.0 | 0.003 |
| | Middle occipital g. | 19 | − 24 | − 87 | 10 | 3.9 | 0.02 | 33 | − 81 | 4 | 3.9 | 0.02 |
| | Lingual g. | 18/17 | − 27 | − 79 | − 9 | 4.1 | 0.009 | 18 | − 82 | − 1 | 4.4 | 0.006 |
| SfM > Random | Superior parietal l. | 7 | − 24 | − 58 | 61 | 5.0 | 0.007 | 27 | − 47 | 60 | 4.3 | 0.013 |
| | Postcentral g. | 5 | − 30 | − 43 | 66 | 3.9 | 0.014 | 30 | − 43 | 68 | 4.3 | 0.014 |
| | Precuneus | 7/19 | − 24 | − 71 | 39 | 4.5 | 0.01 | 18 | − 82 | 43 | 3.9 | 0.014 |
| | Middle frontal g. | 6 | − 18 | 3 | 55 | 4.6 | 0.01 | 27 | − 3 | 55 | 4.7 | 0.01 |
| | Cingulate g. | 31 | − 12 | − 18 | 40 | 4.3 | 0.013 | 15 | − 33 | 40 | 4.6 | 0.01 |
| | Middle temporal g. | 37 | − 48 | − 55 | 3 | 4.1 | 0.014 | | | | | |
| | Middle occipital g. | 39/19 | − 45 | − 80 | 26 | 4.1 | 0.014 | | | | | |
| | Inferior parietal g. | 40 | − 65 | − 30 | 37 | 3.7 | 0.014 | 50 | − 36 | 43 | 3.9 | 0.014 |
| | | | | | | | | | | | | |
| *Children* | | | | | | | | | | | | |
| Random > Static | Middle occipital g. | 18 | − 36 | − 84 | 10 | 4.1 | 0.056* | 33 | − 81 | 4 | 3.9 | 0.056* |
| | Middle temporal g. | 39 | − 45 | − 75 | 15 | 3.5 | 0.057* | 45 | − 73 | 1 | 3.6 | 0.056* |
| | Lingual g. | 17 | | | | | | 9 | − 87 | − 1 | 4.1 | 0.056* |
| SfM > Random | Lingual g. | 18/19 | − 30 | − 64 | 1 | 5.5 | < 0.001 | 30 | − 76 | − 4 | 5.1 | 0.001 |
| | Middle occipital g. | 18/19 | − 27 | − 81 | 15 | 4.5 | 0.003 | 36 | − 75 | 15 | 4.8 | 0.002 |
| | Cuneus | 18/19 | − 21 | − 89 | 29 | 4.8 | 0.002 | 21 | − 90 | 24 | 4.3 | 0.004 |
| | Precuneus | 7 | − 24 | − 74 | 37 | 4.0 | 0.006 | 24 | − 75 | 45 | 4.0 | 0.006 |
| | | | | | | | | | | | | |
| *Adults > Children* | | | | | | | | | | | | |

| **Effect** | **Area** | **BA** | **Coordinates LH** | | | ***Z*** | ***p*-value** | **Coordinates RH** | | | ***Z*** | **p-value** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | ***x*** | ***y*** | ***z*** | | | ***x*** | ***y*** | ***z*** | | |
| SfM > Random | Inferior parietal l. | 40 | − 57 | − 45 | 39 | 3.9 | 0.001 | | | | | |
| | Precuneus | 7 | − 15 | − 47 | 52 | 3.9 | 0.057* | | | | | |
| | | | | | | | | | | | | |
| *Children > Adults* | | | | | | | | | | | | |
| Random > SfM | Precentral g. | 4 | − 36 | − 15 | 45 | 4.2 | 0.046 | | | | | |
| SfM > Random | Lingual g. | 18 | | | | 4.3 | 0.006 | 30 | − 76 | − 4 | 4.3 | |

**Table 1: Talairach coordinates (*x*/*y*/*z*) are listed from left (LH) and right hemisphere (RH) local maxima of significant clusters (FDR corrected $p < 0.05$, * represents trends to significance). *Z*-values are listed for voxels at the local maxima. BA is the Brodmann area nearest to the coordinate and should be considered approximate (g. is gyrus, l. is lobule).**

In a more general analysis, we separated the ROIs into larger functional areas to investigate whether RM affected shape or motion areas differently in children than in adults. Figure 7B shows neural responses to RM (dark grey) in motion (orange), shape (blue) and shape/motion related areas (orange/blue). The data suggests a larger difference between motion and shape related areas in adults than in children during RM perception (dark gray). This observation was confirmed in a significant interaction between age and visual feature specialized area ($F_{1,18}$ = 21.4, $p < 0.001$). This result indicated that RM enhanced activity specifically in motion areas of adults, whereas children showed less neural specialization.

To further investigate whether RM related activity depended on age, we calculated regression coefficients on age within ROIs (Figure 7C). We found significant age-dependent increases in V3a activity (regression coefficient $R^2 = 0.3$, $p=0.01$). A slightly better fit was found for a logarithmic increase in activity within V3a than for a linear increase ($R^2=0.27$, $p=0.02$). No other area showed correlations between age and brain activity (hMT+ $R^2=0.13$, $p=0.11$; all other $R^2<0.05$, $p>0.5$). Thus, neural specialization could be shown by larger differences in response to RM between motion and shape areas in adults than in children, but particularly in dorsal area V3a.

### *6.4.2 Structure-from-motion*

Functional brain imaging data in adults replicated findings that SFM enhanced neural activity as compared with RM in several areas related to shape processing, and also in areas not involved in elementary shape or motion perception, particularly on the occipitotemporal and occipitoparietal junction and further upward into the dorsal stream of the parietal cortex (Figure 6A). The former areas probably correspond with VIPS/POIPS (Orban, Sunaert et al. 1999) or POJ (Paradis, Cornilleau-Peres et al. 2000). The latter area corresponds with PSA (Murray, Olshausen et al. 2003), cIPS (James, Humphrey et al. 2002), or DIPSL/DIPSA (Orban, Sunaert et al. 1999). In children, however, SFM yielded enhanced activity in dorsal and ventral parts of the occipital cortex, but not in the parietal lobule (Figure 6B).

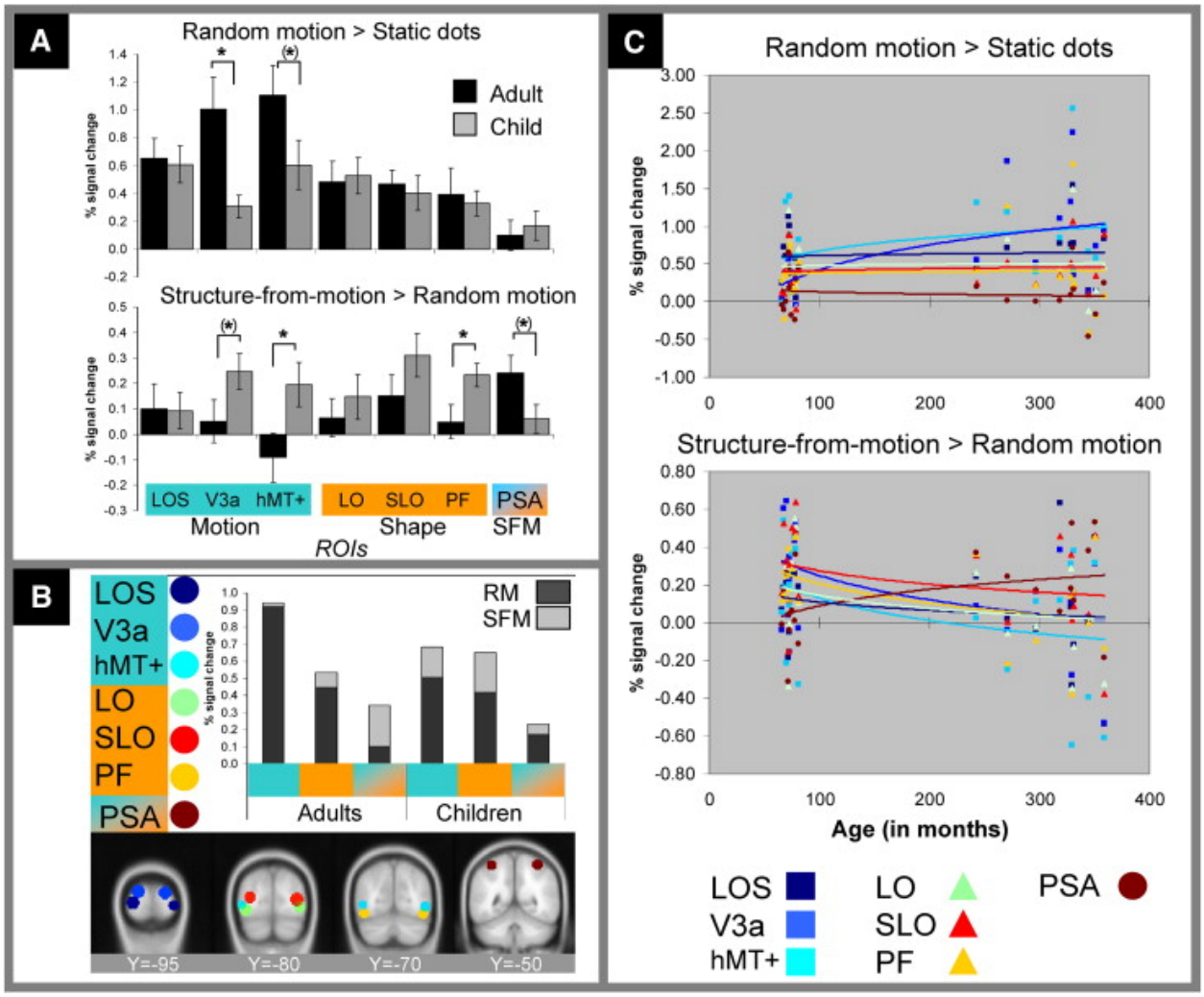


**Figure 8: (A) The top part shows percent signal changes for adults and children for random moving (contrasted against static dots) in regions of interest related to motion processing (blue: LOS=lateral occipital sulcus, V3a=visual area 3a, hMT+=middle temporal area) or shape processing (orange: LO=lateral occipital, SLO=superior lateral occipital, PF=posterior fusiform) or shape and motion processing (blue/orange: PSA=parietal shape area). The bottom part shows the same for the contrast structure-from-motion against random motion. Significant and trends to significance for age-related group differences are marker by asterisk and asterisks in brackets. (B) The ROI locations are illustrated on coronal slices of a canonical brain. The bar plot indicates percent signal change in motion (blue), shape (orange) and shape/motion (blue/orange) -related areas for random motion (RM) against static dots and the additional neural activity that is induced during structure-from-motion (SFM) perception. (C) Percent signal changes for the contrast random>static and structure-from-motion>random-motion plotted against age (in months). The best fit (logarithmic) regression on age is plotted for each ROI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)**

Whole head analysis yield group differences for SFM. Adults showed enhanced neural activity as compared to RM in the inferior and superior parietal lobule (detailed results are listed in Table 1). The superior parietal activity was

located medial and superior to area PSA in Brodmann area 7, whereas the left lateral area was located in the inferior parietal lobule on the border of the precentral gyrus in Brodmann area 40. In contrast, SFM yielded enhanced neural activity in children in the lingual gyrus on the border of the parahippocampal gyrus and fusiform gyrus. This area partially overlaps with area PF. Activity was primarily found in the right hemisphere, but at a lower statistical threshold ($p<0.005$) also left fusiform activity was found. The areas may be identical or adjacent to area posterior part of LO as reported earlier (x = -36, y = -71, z = -13) (Grill-Spector, Kushnir et al. 1999) or with ventral surface areas involved in motion and shape processing (Braddick, O'Brien et al. 2000).

The ROI analysis (Figure 7A) showed that adults and children exhibited different responses to SFM in some but not all areas (Interaction ROI $\times$ GROUP: $F_{6,108}= 4.2$, $p=0.004$). SFM induced enhanced activity in adult PSA ($p<0.003$), but not in children (n.s., adults > children $p=0.057$). In contrast, SFM enhanced neural activity in children more than adults in areas hMT+ (children $p=0.051$; adults n.s.; children > adults $p=0.042$) and PF (children $p=0.001$; adults n.s.; children > adults $p=0.035$).

In a more general analysis, we separated the ROIs into larger functional areas to investigate whether SFM affected shape or motion areas differently in children than in adults. Figure 7B suggests that SFM enhances neural activity in shape related areas more strongly than in motion related areas. This observation is supported by a significant interaction between shape vs. motion related ROIs (excluding PSA) and SFM-RM ($F_{1,18} = 5.2$, $p=0.034$). We found no significant group effect or interaction between shape vs. motion related ROIs and group. This result indicates that both adults and children recruit neural activity in shape related areas during SFM perception.

To further investigate whether SFM related neural activity dependent on age, we calculated regression coefficients on age within ROIs after averaging the percent signal change over the left and right hemisphere ROIs (Figure 7C). We found significant results and trends to significance for an age dependent logarithmic decrease in neural activity in motion processing related areas hMT+ ($p=0.04$) and V3a ($p=0.07$) and shape related area PF ($p=0.03$). This decrease indicated that these areas exhibited enhanced activity for SFM as compared with RM in children, but that this activity attenuated in the maturing brain. On the other hand PSA showed a trend to a logarithmic increase in activity ($p=0.06$), which indicated that

SFM enhanced neural activity in PSA in more mature subjects. Except for area PF ($R^2$=0.23) all areas ($R^2$: hMT+ = 0.21, V3a= 0.17, PSA= 0.18) showed a better fit for a logarithmic age dependent change in activity than for a linear change. Together, the results indicate that SFM enhanced neural activity as compared with RM in dorsal areas within the parietal lobule in adults. Children on the other hand showed enhanced activity under same conditions within dorsal and ventral areas of the occipital lobe that are related to motion and shape processing, including areas that may not be fully mature such as areas hMT+ and V3a. Parietal areas showed no significant neural activity during perception of SFM in children.

## 6.5 Discussion

The aim of the current study was to investigate the neural basis of development in visual perception. As far as we know, this is the first study to show direct evidence that neural activity in the dorsal stream of the occipital cortex and parietal lobule was not mature by the age of 6 years. We also suggest that age dependent neural activity depends on the complexity of the motion stimulus and that high order processes are substituted by low order processes in the immature brain. These claims are discussed in more detail.

In line with previous studies we found that RM activated areas in the ventral and dorsal part of the occipital lobe (Cornette, Dupont et al. 1998; Sunaert, Van Hecke et al. 1999). Ventral activity was found in the lingual gyrus (predominantly in the right hemisphere), whereas dorsal stream activity was found in areas V3a, LOS and hMT+. There was clear evidence that differences in neural development of visual perception can be linked to the dorsal stream. Adults showed neural specialization within dorsal brain areas, particularly area V3a, whereas children activated both dorsal and ventral areas, with less apparent neural specialization. For SFM a different pattern was found. SFM increased activity as compared with RM in both adults and children in the left lateral part of the middle occipital gyrus (SLO) and a dorsal area at the parietooccipital junction. Adults showed enhanced SFM related neural activity only in dorsal areas, including several areas within the parietal lobule, whereas children enhanced neural activity during SFM perception in dorsal and ventral stream areas of the occipital cortex. These data provide evidence for maturation in the parietal lobule and are in line with general anatomical delayed

development of the M-pathway in the dorsal stream including the parietal lobule, which showed that grey matter does not reach maturity by the age of 6 years (Braddick, Atkinson et al. 2003; Gogtay, Giedd et al. 2004; Sowell, Thompson et al. 2004). For the frontal cortex it has been suggested that task unrelated activity decreases during maturation, whereas task related activity increases (Bunge, Dudukovic et al. 2002; Schlaggar, Brown et al. 2002; Booth, Burman et al. 2003; Casey, Tottenham et al. 2005). As far as we know, this is the first study to show that a similar developmental mechanism occurs within the parietal lobule and in area V3a within the dorsal part of the occipital cortex.

The second question was whether developmental differences were stimulus dependent and limited to high order visual processing. The present results support this hypothesis. First, RM and SFM showed developmental effects in different areas. Area V3a showed age dependent differences in response to RM, whereas areas in the parietal lobule showed age related differences in response to SFM. There was no area that showed common age dependent difference related to RM and SFM. Second, the same area V3a that was not specifically activated in children during RM perception showed enhanced activity during SFM perception, which strongly suggests that neural activity in area V3a depends on both maturation and stimulus complexity. Third, age dependent effects related to SFM perception were different in high order processing areas than in areas related to motion and shape processing. Areas in the parietal lobule were only activated by adults, whereas common neural activity was found in both age groups on the occipital parietal junction, suggesting that both groups similarly processed coherent motion (Paradis et al. 2003). Children, however, showed increased neural activity during SFM perception in shape and motion related areas. Thus, we assert that children and adults use different neural mechanisms in the perception of high order visual stimuli and that age related differences in neural activity arise from the high order visual features of the SFM stimulus.

It remains an open question as to whether increased activity in children in the occipital lobe during SFM has a functional role in perception. Behavioural developmental studies show that SFM can be detected by infants (Arterberry and Yonas 2000) and reach a mature level at the age of 7 (Parrish, Giaschi et al. 2005). Dependent on the perceptual features and the attentional demands during the task, however, developmental differences occur even until adolescence (Schrauf, Wist et al. 1999). In our task we used passive viewing instructions, so that the perceptual

demands are low, but the relation to perceptual performance and attentional demands are unclear. Thus, given that perceptive capabilities are different between adults and children, and that children can principally perceive SFM stimuli, we tend to suggest that reduced maturation is substituted by increased neural activity in areas involved in feature specific analyses, whereas the engagement of adult dorsal areas in the parietal lobule during SFM perception relates to maturation. The relation between neural activity in these areas and perceptual capability remains to be answered in future studies.

The present results partially differed from previous studies. For example, in contrast to Murray and colleagues (2003) we found no reduced activity in V1 by SFM as compared with RM. They argued that SFM induced a top-down suppression of V1 activity. In contrast to that study we did not use an attention demanding perceptive task. Studies that used a passive viewing task, reported no stimulus dependent V1 difference in activity (Paradis, Cornilleau-Peres et al. 2000). Our results are in line with the latter findings. Further, we found no direct evidence that SFM activated motion processing related areas. SFM did not significantly enhance areas related to RM in adults, though it enhanced shape processing related areas. This result contrasts with Murray and colleagues (2003) who showed increased activity in area hMT+ by SFM in adults. Again, these results may be related to the use of a passive viewing task, since they are in line with findings that SFM does not enhance neural activity in hMT+ when a passive viewing task is used (Paradis, Cornilleau-Peres et al. 2000).

Another difference between the current and several other studies with adults on high order perception is that we used no coherent motion condition. We know from previous reports that such stimuli activate intermediate areas within the dorsal stream on the border of the occipital and parietal cortex (Orban, Sunaert et al. 1999; Braddick, O'Brien et al. 2000; Paradis, Cornilleau-Peres et al. 2000; Braddick, O'Brien et al. 2001). Since we scanned young children we were limited in scanning time (approximately 12 minutes). We thus chose to use a more complex condition of 3D SFM instead of a coherent motion condition to contrast with RM. Future studies are needed to provide a more fine-grained analysis of neural development.

Other aspects might cast doubt on our conclusions. First, it is not trivial to spatially normalize young children with an adult anatomical template. Yet, the present results seem to be anatomically valid. Structural imaging studies reported

that particularly the parietal and frontal cortex differ in both grey and white matter (Sowell, Trauner et al. 2002). The present results support a functional-anatomical development particularly in the parietal lobule, which cannot be entirely attributed to general differences in brain activity, since children show some activity in these areas in the contrast between RM and static control stimuli. Rather, these age-related differences are stimulus specific. Further, the normalisation procedures as applied here are in line with normalisation comparison studies. Two studies reported that both timing and peak activations were comparable between 7 to 8 year old children and adults after normalization into a common stereotactic space (Kang, Burgund et al. 2002). The children tested here were one to two years younger than in those studies. We further showed in an individual subject analysis that activity within ROIs was present in both adults and children, but that the level of neural activity differed. This suggests that functional brain areas in children were not spatially shifted as compared with adults. Nevertheless, the way in which maturation is expressed in neural activity in younger children is still under debate, and cannot be entirely solved here.

Secondly, children may have used different eye movement strategies during perception than adults, which might have biased imaging results based on the lack of eye tracking control and long stimulus presentation. The relation between eye movement and perception is an issue on its own. In the current study we preferred to minimize control over eye movement in order to not bias potential perceptual control mechanisms, which may differ between adults and children. Thirdly, stronger head movement during the task in children may bias fMRI results. Clearly, children moved generally more than adults, but no child moved beyond acceptable ranges and we found stimulus dependent neural activity that cannot be explained by movement alone. Fourth, children listened to a story while viewing whereas adults did not. This might be a potential confound inducing cross modal interference. However, the story barely exceeded scanner noise and could hardly be heard so that it is unlikely to interfere with neural activity during visual processing. Another reason is that the effect on visual processing is small. An interaction between highly demanding processing condition (mental imagery) and rest could only be verified in visual cortex in a PET study when scanner noise was compared with a no noise condition. Only after ROI analysis in the cuneus a task by condition effect could be shown (Mazard, Mazoyer et al. 2002). Thus, there is little reason to believe that these factors biased the main results. Taken together, the current

study provides evidence that dorsal brain areas are not fully developed in six year old children, even during simple motion perception. Perception of SFM stimuli engages high order brain areas that show structural changes in neural development, whereas low order feature specific brain areas are used less with increasing maturation.

## 6.6 Acknowledgement

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# 7 Neural development of biological motion perception in preschool and school age children (5-7)[2]

**Lichtensteiger J**, **Bucher K**, **Loenneker T**, **Martin E**, **Klaver P**

## 7.1 Abstract

The perception of biological motion (BM) - of other individuals' movements - is an essential skill of daily social interaction. BM perception has been associated with neural activity in the right posterior superior temporal sulcus (pSTS) representing a pivotal point of the dorsal and ventral stream. Little is known about how areas within these two streams develop functionally. We explored developmental changes in neural substrates for BM perception, using event-related fMRI. Children (age 5-7 years) and adults (age 20-32) performed a perceptual task with BM, BM in snow (BM_s) using coherently moving background noise as distractors and equivalent scrambled motion (SM/SM_s) stimuli. BM elicited faster reaction times (RTs) than SM in both groups. In children, RTs were slower and they showed lower accuracy rates than adults. During BM perception adults showed activation in dorsal (cuneus, precuneus and supramarginal gyrus) and ventral areas (lingual gyrus, fusiform gyrus and hMT+) of the visual system as well as in pSTS predominately in the right hemisphere. For the same condition children only activated the right fusiform gyrus. Group comparisons indicated increased activation in right pSTS and bilateral parietal regions in adults for BM perception. Likewise children showed enhanced activation in fronto-parietal regions of the left hemisphere when BM_s was presented. The present findings indicate that the development of task-specific dorsal stream functioning is not complete at age six. Thus, only adults activated the expected dorsal and ventral regions including pSTS during BM perception, whereas children seem to recruit networks within the ventral stream. Furthermore, only children engaged dorsal (parietal) and frontal regions during task conditions with increased level of attention such as in the perception of BM in snow.

Keywords: Development, ventral and dorsal stream, biological motion perception, fMRI

[2] to be submitted to Developmental Science

## 7.2 Introduction

The perception of other individuals' movements, actions, intentions and identities is essential for successful interactions in a social environment. Adults are highly sensitive in recognizing human kinematics and identifying different actions even in displays that only contain very reduced information of human movements. Patterns of movement generated by living forms can also be determined as biological motion (BM). Early work performed by Johansson (Johansson 1973) demonstrated that illuminating the major joints and head of a walking person is sufficient to convey a vivid impression of human movements, despite the percept collapsing into a meaningless stimulus when the actor stands still. From such displays various action patterns (Dittrich 1993), gender (Mather and Murdoch 1994) and even facial expressions (Bassili 1978) can be determined.

Sensitivity to BM stimuli is considered to occur very early in perceptual development. Experiments of BM perception in infants (Fox and McDaniel 1982; Bertenthal, Proffitt et al. 1987; Bertenthal and Pinto 1994) revealed that at 3-5-months of age children start to show a preference for BM. Beyond infancy there are only a few studies comparing the sensitivity. to BM of typically developing children and adults. In studies including young children, they generally served as an age matched control group for the comparison to a clinical population such as autistic children (Blake, Turner et al. 2003), children suffering from Williams Syndrome (Jordan, Reiss et al. 2002) or adolescents with motor impairments associated with periventricular leukomalacia (PVL) (Pavlova, Staudt et al. 2003). There are only a few studies that provide evidence on the sensitivity of typically developing children to BM. Pavlova et al. (Pavlova, Krageloh-Mann et al. 2001) found that 3-year-olds were able to recognize a walking person in a point-light display but performance linearly increased up to the age of five. Likewise, no correlation between age and accuracy (of performance) could be detected in a study of typically developing 5- to 10-year-old children (Blake, Turner et al. 2003). Most probably ceiling levels were reached early in these studies. Thus, differences in sensitivity to BM have been observed between children over 5 years of age and adults only when point-light animations were embedded within an array of dynamic noise dots (Jordan, Reiss et al. 2002; Blake, Turner et al. 2003; Freire, Lewis et al. 2006) – which has previously been used to make the

recognition of BM more demanding (Bertenthal and Pinto 1994; Pavlova, Krageloh-Mann et al. 2001; Ikeda, Blake et al. 2005).

Little is known about how the neural structures seemingly involved in BM processing develop and how development of these structures is correlated with behavioral performance. Previous neurophysiological and neuroimaging studies of adults indicate that the extrastriate area most closely associated with its integrating function in the perception of BM is the posterior region of the superior temporal sulcus (pSTS) (Grossman, Donnelly et al. 2000; Grezes, Fonlupt et al. 2001; Vaina, Solomon et al. 2001; Beauchamp, Lee et al. 2003; Puce and Perrett 2003). Additional areas identified in adults include the motion-sensitive region MT (Vaina, Solomon et al. 2001; Beauchamp, Lee et al. 2003), the parietal cortex (Grossman, Donnelly et al. 2000; Grezes, Fonlupt et al. 2001; Puce and Perrett 2003), the fusiform gyrus (Grossman and Blake 2002) as well as the lingual gyrus (Servos, Osu et al. 2002).

These regions are also linked to a functional concept of dividing the human visual cortex into two cortical visual systems (Milner and Goodale 1996). The ventral system preferentially responds to visual stimuli such as objects, faces or places and is located in the occipital and temporal lobe. The other system being settled in the dorsal occipital and parietal lobe is known to respond to visual motion and is relevant in recognizing the localization of an object. Recent theories indicate that both systems are involved in the recognition of BM. It seems likely that the dorsal pathway, which is specialized for the processing of motion information, contributes substantially to the perception of BM (Mather, Radford et al. 1992). At the same time, subjects can recognize gait patterns from individual stationary key frames (Todd 1983) indicating that also the ventral pathway is involved. Neuroimaging data provides evidence that BM processing confluences activity from the dorsal and the ventral stream brain areas with the pSTS representing a pivotal point within this network (Shiffrar 1994; Giese 2004).

Discovery of these two functionally divided streams has generated debate about the development of functional specialization. Anatomical and MRI evidence indicate that extrastriate visual cortex development continues until late adolescence (Giedd, Blumenthal et al. 1999). However, results about a distinct development of dorsal and ventral stream functions in these extrastriate regions are contradictory. On the one hand, faster dorsal stream development was

proposed (Dobkins, Anderson et al. 1999) but on the other hand, slower dorsal stream development was reported (Atkinson 1992). Psychometric studies with children aged 6 to 16 years showed that color thresholds decrease to reach adult levels at about puberty onset but motion thresholds remain higher than adults' across this age range (Hollants-Gilhuijs, Ruijter et al. 1998; Hollants-Gilhuijs, Ruijter et al. 1998) indicating that the dorsal pathway may show more protracted development than some abilities related to the ventral pathway. Additionally, motion coherence processing develops more slowly than form processing (Gunn, Cory et al. 2002; Bucher, Dietrich et al. 2006). In studies comparing children and adults on tasks that are dependant on extrastriate cortical (applying dorsal or ventral pathways) structures it has been concluded that at least some aspects of dorsal pathway functions are slower to develop than ventral pathway functioning (for summary see (Johnson, Mareschal et al. 2001)).

The amount of neuroimaging and neurophysiological studies investigating BM perception in children is very limited and furthermore conflicting results were found. Some studies found little evidence for developmental changes. Accordingly, Mosconi et al. (Mosconi, Mack et al. 2005) detected no differences in functional activation patterns between adults and 7-10-year-old children while observing eye gaze shifts. Furthermore, ERP studies provide evidence that both adults and 2-8 years old children engage similar networks during the perception of human and object movements (Cochin, Barthelemy et al. 2001). In another neurophysiological study, BM evoked similar right hemispheric activation patterns in 8-months-old infants and in adults (Hirai and Hiraki 2005). Moreover, infants of the same age process upright and inverted BM figures differently (Reid, Hoehl et al. 2006) indicating that already infants process BM in a very specific way. In contrast, Carter and Pelphrey (Carter and Pelphrey 2006) detected reduced activity in pSTS in response to BM stimuli when they compared functional activity in 7-10 year-old children and adults. Moreover, from neuroimaging studies on the development of face perception we know that both preschool (5 - 8y) and school age (9 - 11 y) children show ventral stream activity but only the school age children activated FFA (Gathers, Bhatt et al. 2004) and that functional activity shifts from bilateral and more widespread to a more localized profile (Passarotti, Smith et al. 2007). These results indicate that also ventral stream functioning is not mature at preschool age. Furthermore, studies on the development of visual motion processing reported that both activation pattern

(Bucher, Dietrich et al. 2006; Klaver, Lichtensteiger et al. 2008) and electrophysiological responses (Bucher, Dietrich et al. 2006) develop up to adolescence suggesting that also functional dorsal stream development undergoes substantial progression from infancy to adulthood.

In this study, we used event-related fMRI to examine the functional development of extrastriate areas involved in processing BM by comparing the activation pattern of 5-to-7-year-old children and adults. Since behavioral differences between adults and children above 5 years of age were only for BM stimulus presented within an array of distracting moving dots (BM_s) (Freire, Lewis et al. 2006), we further aimed to investigate the influence of distrators on developmental effects. It is also known that in adults masking visual stimuli affects the neural activity within task-specific areas (Grossman, Blake et al. 2004). We therefore predict that neural activity in task-specific areas decreases in adults as well as in children. To this end, the task of the current study involved BM, scrambled motion (SM), BM with distractors (BM_s) and scrambled motion with distractors (SM_s).

Based upon behavioral, anatomical, neurophysiological and neuroimaging results (Huttenlocher 1990; Atkinson 1992; Giedd, Blumenthal et al. 1999; Gunn, Cory et al. 2002; Bucher, Dietrich et al. 2006; Carter and Pelphrey 2006; Wilke, Krageloh-Mann et al. 2007) of dorsal and ventral stream development we predict that for BM processing in children, as young as in our group, functional activity within dorsal regions may be alternated by engagement of earlier maturing networks within the ventral stream. With accumulated experience and maturation, dorsal regions will then become increasingly involved in BM processing. Furthermore it is known that in children, task-unspecific activation decreases and task-specific activation increases with development (Booth, Burman et al. 2001; Casey et al. 2002). We therefore expect the children to show additional activity within fronto-parietal areas regions, which incorporates a rather task supportive than task-specific function.

## 7.3 Materials and Methods

### *7.3.1 Participants*

21 adults and 23 children were recruited from the local community. All participants had normal or corrected-to-normal vision and were screened against neurological and psychiatric illnesses. A local ethics committee approved this study. fMRI data from 3 adults and 4 children were discarded due to technical problems, and data from 6 children were excluded because of excessive head motion (over 4mm in either x-, y- or z-plane). The final data set included 18 healthy adult volunteers (10 females) [mean age = 27.54 ±3.7 years] and 13 children (5 girls) [mean age = 6.59 ±1.2 years].

### *7.3.2 MRI and fMRI scanning procedures*

All participants underwent a short behavioral practice session before the brain imaging session to assure that task instructions were understood and BM could be discriminated from SM. The imaging session lasted approximately 25 minutes. Subjects were fitted with earplugs and additional acoustic noise protection was given by headphones (MRI Audio/Video System, Resonance Technology, Inc., USA). The head was padded to minimize head movements. We used MR-compatible video goggles to present the stimuli. Participants used a 2-button response box with fiber optic connections to indicate their decision (Lumina LP-400, Cedrus Cooperation, San Pedro, USA).

BOLD sensitive images were collected on a 3.0 T General Electric MR-scanner using a gradient-echo EPI-sequence with a repetition time of 2500 ms and 32 slices were aligned to the anterior and posterior commissure (flip angle = 50º, FOV= 22cm, 64x64 matrix, slice thickness per volume = 2.7mm, 246 repetitions). A three dimensional T1-weighted anatomical scan (FOV = 230 mm x 198 mm x 158 mm, matrix = 224x192x132; TR = 8.6 ms; TE = 2.1 ms) of the whole brain was acquired.

### *7.3.3 Preparing children for scanning*

Children were slowly introduced to the scanner and its equipment. For all children, a teddy bear was positioned on the scanner table in order to explain the scanning procedure to the child in an attempt to ease reservations about the procedure and alleviate anxiety. While all subjects were wearing some form of sound attenuation and hearing protection we additionally equipped the inside of the scanner with a sound diminishing foam mat whilst children were measured. Children were able to watch a cartoon video during localizer and anatomical acquisitions. Parents stayed outside the scanner room but were able to talk to the child between the scans.

## 7.4 Experimental design

Participants were scanned as they viewed point-light BM animations (see FIG 1) depicting a front-view of three different human actions (walking, jumping and waving) [BM], scrambled versions of the same animations [SM] and point-light BM animations masked by noise dots representative of BM in snow [BM_s]. The fourth condition consisted of scrambled versions of the same animations also masked by noise dots [SM_s].

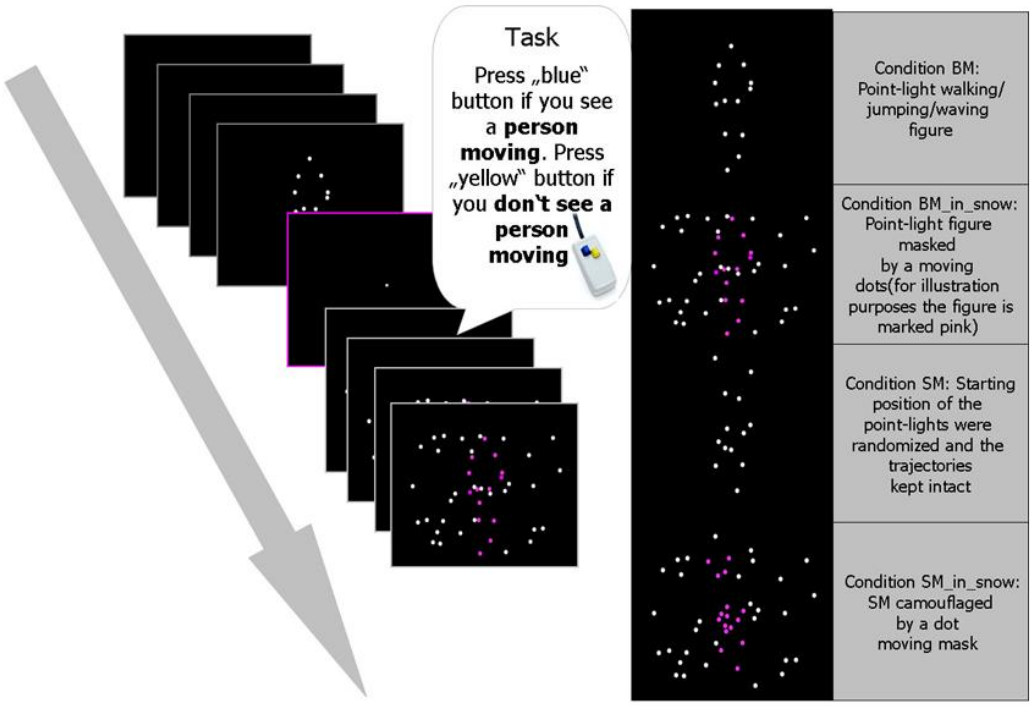


**Figure 9: Task stimuli and presentation. The presentation of the trials was randomized across subjects.**

A resting condition (fixation) was used as a baseline. Point-light BM sequences were taken from a selection of the standardized point-light pictures (Vanrie and Verfaillie 2004). Scrambled point-light images were created by using an in-house written Matlab® script. These images were generated by permuting and randomly shifting the starting position of the point-lights while keeping the trajectories intact, except that each point-light trajectory was randomly rotated in 900 increments and/or mirrored. The rotation and reflectance of dots during scrambling additionally disrupts local form information that may remain after spatial scrambling. The starting positions were chosen within a region such that the total area encompassed by the figure was similar to that of the BM figures (see Figure 8). BM_s/SM_s was created by adding 33 randomly distributed dots of equal size as in BM stimuli that were continuously shifted between frames with a velocity of 360° divided by the number of frames and a pseudo randomized offset angle of 5% divided by the number of frames to 15% divided by the number of frames of the image size. The number of frames reflect the total number of images of the sequence. The snow trajectories were equal for both,

the BM and SM sequences. The experiment was programmed using Presentation (www.neurobs.com). Subjects were instructed to press the right button when they detected a person moving (finding "the man in the snowstorm") and the left button to indicate when they perceived no human motion, with their right index and middle finger, respectively. All subjects were instructed to answer as soon and as accurately as possible.

## 7.5 Data analysis

### *7.5.1 Data preprocessing*

The two initial EPI scans were discarded to allow for T1 saturation effects. Using SPM2 (Wellcome Department of Cognitive Neurology, University College London Medical School, London, UK; www.fil.ion.ucl.ac.uk/spm/) functional images were realigned and unwarped to correct for motion artefacts. Incorrect and missed responses were excluded from analysis since it has been demonstrated that even a small number of errors might alter activation maps (Murphy and Garavan 2004). No individual run had more than 4mm maximum displacement in x-, y-, and z-plane. Individual T1-weighted anatomical images were taken for coregistration with the functional images. According to recent studies that have tested the possibility to generalize results across age for adults and 6 and 7 year old children (Kang, Burgund et al. 2002; Klaver, Lichtensteiger et al. 2008), we transferred functional and anatomical data of adults and children into a common stereotactic space. To this end, T1-weighted anatomical images were segmented and the normalization parameters were estimated for grey matter images on standard grey matter template in Montreal Neurological Institute (MNI) space. Both EPI (to 3mm3 voxels) and T1-weighted (to 1mm3) images were normalized. EPI images were then spatially smoothed using a 9 mm full width at half maximum (FWHM) Gaussian kernel and temporally filtered (high-pass 128 s cut-off).

### *7.5.2 Statistical analysis*

The hemodynamic response was modelled by a stick function (general linear model) to each stimulus presentation in each category convolved with a canonical hemodynamic response function and its temporal derivative. Parameter images were generated for the contrasts BM, BM_s, SM and SM_s in each subject. We applied planned t-tests in a second level random-effect analysis for the contrasts BM>SM and BM_s>SM_s. To investigate whether maturation or the presence of distractors affected the network of brain areas involved in BM perception we masked the within and between group comparison by the contrast BMall (BM + BM_s) > SMall (SM + SM_s) across groups. For the within group comparisons significant voxels are reported ($p<0.001$) for clusters of 5 voxels, which was the threshold of a significant cluster after correction for multiple comparisons ($p<0.05$) within the regions of interest. For the between group comparison (adults > children, children > adults) the HDR peak difference was set at $p<0.001$ ($k\geq5$, two-tailed, uncorrected). The results are listed in Table 1. For illustrating purposes thresholds of within- and between-group results are set at $p<0.05$ ($k\geq20$, two-tailed, uncorrected) in Figure 10.

## 7.6 Results

### *7.6.1 Behavioural Data*

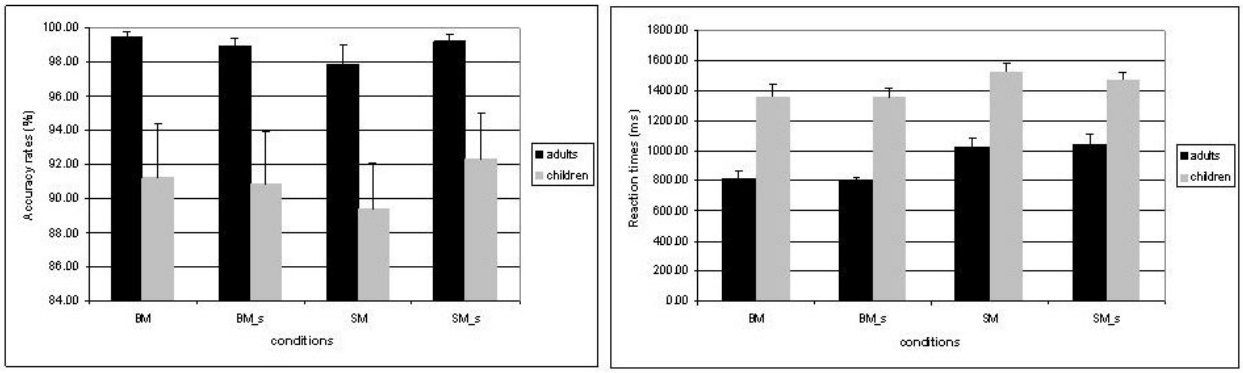


**Figure 10: Accuracy rates and reaction times of children and adults across all conditions.**

Performance was assessed by reaction time [RT] and accuracy rate [AR] (see Figure 9). A two-way repeated-measures ANOVA on reaction times with the within-subject-factors condition (BM/SM) and noise (snow/nosnow) and the between-subject factor group (adults/children) indicated a significant effect of condition ($F_{1,29} = 50.96$; $p < 0.001$) with shorter RTs for BM than for SM in both groups. There was also a significant main effect of the factor group ($F_{1,29} = 57.36$; $p < 0.001$) with adults showing faster reaction times across all conditions. Additionally, we found a tendency for the interaction between condition and group ($F_{1,29} = 2.96$; $p < 0.1$). Children tended to have faster RTs for BM than SM whereas the RT of adults did not differ between conditions. The results of AR revealed a significant main effect of the factor group ($F_{1,29} = 15.13$; $p < 0.001$). Children made significantly more mistakes than adults but both groups performed above 89% correctness. There were no effects of condition and noise (snow / no snow) or interactions between or within subject factors.

### *7.6.2 fMRI results*

Brain regions showing significant responses to BM and BM_s are listed in Table 2 for within- and between- group comparison separately.

| | Region | *k* | Hemi | MNI coordinates | | | *p* FDR-corr. | SPM | BA |
|---|---|---|---|---|---|---|---|---|---|
| | | | | *x* | *y* | *z* | | | |
| **Adults** | | | | | | | | | |
| BM > SM | precuneus | 50 | R | 3 | -42 | 42 | 0.001 | 4.43 | 7 |
| | lingual gyrus | 41 | R | 57 | -63 | 0 | 0.001 | 4.05 | 18 |
| | pSTS | 9 | R | 63 | -45 | 18 | 0.001 | 3.72 | 22 |
| | supramarginal gyrus | 19 | R | 48 | -39 | 35 | 0.001 | 3.69 | 40 |
| | MT | 10 | L | -51 | -72 | 9 | 0.002 | 3.46 | 39 |
| | Fusiform gyrus | 5 | R | 39 | -45 | -21 | 0.002 | 3.42 | 37 |
| | Cuneus | 8 | R | 24 | -93 | 3 | 0.002 | 3.34 | 18 |
| BM_s < SM_s | n.s. activated voxels | | | | | | | | |
| **Children** | | | | | | | | | |
| BM > SM | Fusiform gyrus | 6 | R | 39 | -54 | -15 | 0.04 | 3.44 | 37 |
| BM_s > SM_s | Fusiform gyrus | 7 | R | 42 | -48 | -21 | 0.02 | 3.50 | 37 |
| | supramarginal gyrus | 3 | L | -54 | -42 | 33 | 0.02 | 3.47 | 40 |
| | Middle occipital lobe | 7 | L | -48 | -69 | 9 | 0.02 | 3.23 | 19 |
| **Adults > Children** | | | | | | | | | |
| BM > SM | pSTS | 24 | R | 48 | -20 | 4 | | 3.90 | 22 |
| | precuneus | 32 | L | -3 | -44 | 46 | | 3.84 | 7 |
| | precuneus | 21 | R | 3 | -71 | 45 | | 3.50 | 7 |
| | postcentral gyrus | 65 | R | 62 | -25 | 18 | | 3.82 | 40 |
| BM_s > SM_s | n.s. activated voxels | | | | | | | | |
| **Children > Adults** | | | | | | | | | |
| BM > SM | n.s. activated voxels | | | | | | | | |
| BM_s > SM_s | claustrum | 39 | L | -30 | -2 | 14 | | 4.58 | - |
| | claustrum | 5 | L | -24 | 20 | -4 | | 3.24 | - |
| | anterior cingulate gyrus (ACC) | 54 | L | -9 | 0 | 48 | | 3.49 | 24 |
| | thalamus | 8 | L | -9 | -24 | 15 | | 3.40 | - |
| | medial frontal gyrus | 12 | R | 9 | 14 | 44 | | 3.34 | 32 |

**Tabelle 2: MNI coordinates of the local maxima of adults and children's activation peaks within clusters and group comparison (k = number of voxels)**

### *7.6.3 Within-group-analysis*

*Adults*. When BM and SM responses were compared enhanced neural activity was found within in the right hemisphere in precuneus, in pSTS, in cuneus and in supramarginal gyrus. In the left hemisphere activation was found only in middle temporal gyrus (hMT). Furthermore, significant activation was found in right lingual gyrus and in right fusiform gyrus. When BM_s was compared to SM_s no significant activation clusters could be detected (see Table 2; FIG 10).

*Children*. For the comparison of BM and SM we found enhanced activation patterns only in right fusiform gyrus. When BM_s was compared to SM_s, increased activation was found in right fusiform gyrus and left supramarginal gyrus of the parietal lobe. Additionally, we found increased activation in left middle occipital gyrus.

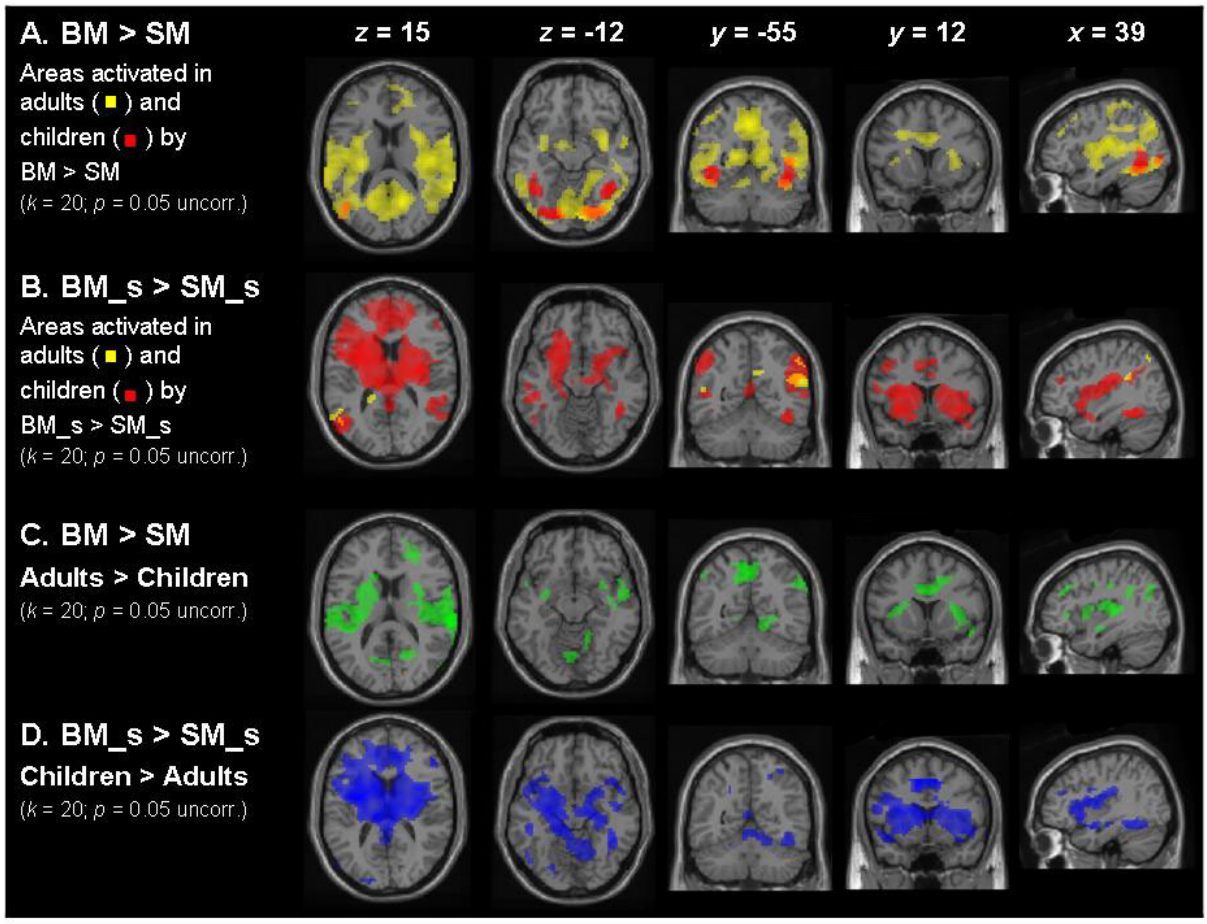


**Figure 11: Statistical maps overlaid on coronal slices of a canonical structural MR image. Displayed are the within-subject contrasts for adults (yellow) and children (red) for BM>SM (A) and BM_s>SM_s (B) ; between-subject contrasts for BM>SM [(C) green, adults>children] and BM_s>SM_s [(D) blue children>adults)]. For illustrating purposes the maps are displayed at a statistical thresholds of *p*<0.05, uncorrected in the whole brain. It shows that adults and children both show significant neural activity in ventral areas (lingual gyrus and FG) but only adults also activated dorsal regions by the perception of BM.**

### *7.6.4 Between-group-analysis*

For the contrast 'BM > SM' the group comparison revealed increased activation in adults as compared to children in right pSTS, bilateral precuneus and right postcentral gyrus. The opposite contrast (children > adults) did not yield any significant activation.

For the contrast 'BM_s > SM_s' children showed more activity than adults in areas of the left claustrum in the left cingulate gyrus, in the left thalamus and in the right medial gyrus of the frontal lobe. No significant differences could be detected for the opposite contrast (adults > children).

## 7.7 Discussion

The aim of the study was to investigate the neural development of BM perception in preschool and school age children and to clarify to which extent successful processing (i.e. perception) of BM is dependant on the development of dorsal stream functioning. We found evidence that task-specific dorsal stream functioning is not yet fully developed at age six. Our data and data from an earlier study of our group (Klaver, Lichtensteiger et al. 2008) go in line with fMRI studies suggesting that maturation and learning correspond to a fine-tuning of neural systems with enhanced recruitment of task-specific regions. In the following, these claims are discussed in more detail.

In accordance with previous studies we found that BM perception in adults elicited activation in dorsal and ventral regions of the occipital, temporal and parietal lobe. Activity was found in pSTS – the area most closely associated with BM perception (Grossman, Donnelly et al. 2000; Grezes, Fonlupt et al. 2001; Vaina, Solomon et al. 2001; Beauchamp, Lee et al. 2003; Puce and Perrett 2003) and pivotal point of the dorsal and ventral stream. Additional loci of dorsal activation were previously identified in studies on BM perception. Additional loci of dorsal and ventral activation were previously identified in studies on BM perception. Dorsal areas include the motion-sensitive region MT (hMT+) (Vaina, Solomon et al. 2001; Beauchamp, Lee et al. 2003), the parietal cortex (Bonda, Petrides et al. 1996; Grezes, Fonlupt et al. 2001; Vaina, Solomon et al. 2001; Santi, Servos et al. 2003) and its postero-medial portion, the precuneus (Ptito, Faubert et al. 2003). Ventral activity was found in right fusiform gyrus and in right lingual gyrus (Vaina, Solomon et al. 2001; Servos, Osu et al. 2002; Ptito, Faubert et al. 2003; Santi, Servos et al. 2003; Pelphrey, Morris et al. 2005). As compared with children adults showed increased functional activity related to BM in dorsal areas including right pSTS, supramarginal gyrus (SMG) as well as right cuneus within the parietal lobe, whereas children only elicited enhanced neural activity in ventral regions such as bilateral fusiform gyrus. These findings suggest that perception of BM may activate both dorsal and ventral streams in adult subjects, whereas children only activate ventral regions for processing BM. The data therefore provide evidence for a more protracted development of task-specific functioning of the dorsal system and are in accordance with anatomical studies, showing that grey matter of anatomical regions located within the dorsal

stream does not reach maturity by the age of 6 years (Braddick, Atkinson et al. 2003; Gogtay, Giedd et al. 2004; Sowell, Thompson et al. 2004). The dorsal pathway hosts more complex functions than the ventral stream. Probably, these functions rather rely on life-long learning (plasticity) whereas ventral stream functions might be more constant. For example, during BM perception dorsal stream areas have to integrate information from sensory systems with propioceptive feedback to generate "body-centered" representations for action. As the body of the child is developing physically, important factors such as length and weight of limbs continue to change. Thus, it may be more important to retain plasticity in the dorsal stream than in the ventral (see (Gilmore and Johnson 1998)) – which, however, makes this pathway more vulnerable to all types of experiences (Coch, Skendzel et al. 2005).

The second question was how noise distractors (BM_s) affects the neural activity within the network of brain areas particularly involved in BM perception in fully developed and maturing brains. When comparing BM_s and SM_s in adults, we could not detect any activity. Although the classical BM network could be found at lower threshold ($p < 0.05$, uncorr.) (see Figure 10). These findings are in accordance with results from an earlier study which could show that pSTS activity is reduced when the stimuli were presented within distractors (Grossman, Blake et al. 2004). Children did not show this reduction in activity. Children activated similar networks for the contrast 'BM_s > SM_s' as for the contrast 'BM > SM' in the FG. However, they further activated fronto-parietal regions such as left claustrum, right medial frontal gyrus, left anterior cingulate (ACC) and left thalamus. Functions attributed to these areas are mostly related to attention, and are thought to incorporate rather task supportive than task-specific functions. The claustrum is generally associated with selective attention modulating visual perception, e.g. visual search tasks (Treisman 1969; Braun and Julesz 1997). The medial frontal gyrus (identified as BA 32) is also called the dorsal region of anterior cingulate gyrus and is linked to rational thought processes, most notably active during the Stroop task (Egner and Hirsch 2005). In a recent study by Olesen et al. (Olesen, Macoveanu et al. 2007) they found that children showed more frontal activity in response to distracters. Probably, the increased frontal activity in children reflects the more attentional demands for the extraction of BM from noise. The ACC seems to be especially involved when effort is needed to carry out a task such as in early learning and problem

solving (Allman, Hakeem et al. 2001). Many studies attribute functions such as error detection, anticipation of tasks, motivation, and modulation of emotional responses to the ACC (Posner and DiGirolomo 1998; Bush, Luu et al. 2000; Nieuwenhuis, Ridderinkhof et al. 2001; Crottaz-Herbette and Menon 2006). Here we note that these findings are not reflected on the behavioral level since children did not show slower reaction times or lower accuracy in the BM_s condition relative to the BM condition although they were generally slower and less accurate than adults.

Taken together, enhanced activations of these specific areas imply that for children the BM_s task was more demanding and therefore they showed increased fronto-parietal activity. Yet, they also showed activity within the BM sensitive network of areas that were limited to the ventral stream. We therefore suggest that in order to show a similar performance pattern as adults, activations within rather task-unspecific structures may serve as compensational processes of an otherwise immature network.

Current findings partially differ from previous studies. For example, in relation to behavioral studies our results do not agree with a study by Freire et al. (Freire, Lewis et al. 2006), that found differences in BM recognition when distractors of different amount of dots were used. In our study a fixed and relatively small number of random noise dots was used. This might explain why we could not detect any behavioral differences between BM and BM_s. Furthermore, in contrast to Mosconi et al. (Mosconi, Mack et al. 2005) we detected differences in activations within the dorsal pathway between children and adults. In opposite to that study our children were about three to two years younger. Furthermore, it is known that activation patterns strongly depend on the task assigned, and since in that study a gaze perception task was used, conflicting results are not surprising. However, our results go in line with previous research examining the functional development of motion-defined form perception in children. In these studies it has been shown that maturation occurs well into childhood and even adolescence (Gunn, Cory et al. 2002). In a motion-defined letter identification task with different velocities, children did not reach adult levels before 7-8 years (Giaschi and Regan 1997; Klaver, Lichtensteiger et al. 2008). Also in a previous study we could show that neural activity within dorsal regions of the occipital and parietal lobule is not mature at age 6 (Klaver, Lichtensteiger et al. 2008).

Additionally, it is noteworthy that children may have used different eye movement strategies during task solution. Since children exhibited more activation in thalamus, most likely the superior colliculi [SC], during perception of BM_s, it is possible that eye movements could have played a certain role in this condition. However, a recent study investigating neural activation increases during free visual search (Grossman, Blake et al. 2004) could show that activity in SC could only be partially explained by oculomotor control. Additionally, we found the frontal eye fields (FEF) whether being activated in children nor in adults (Posner and DiGirolomo 1998). We assume that in the current study eye movement pattern were similar in children and adults.

In summary, in preschool and school age children BM perception engages ventral areas whereas the classical network for BM processing in the dorsal stream is recruited later during development. Therefore we conclude that the functional segregation into dorsal and ventral stream is still immature at the age of 6.

## 7.8 Acknowledgment

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# 8 General Discussion

## 8.1 Functional Plasticity in Visual Motion Processing

In the present Ph.D. the functional development of the neural correlates of visual structure-from-motion and biological motion perception was investigated. The first study (chapter 2) describes the development of the neural correlates of structure-from-motion and the second study (chapter 3) of biological motion perception. Both studies focus on the development of extrastriate areas within the visual system that are known to be activated during structure-from-motion and biological motion perception.

The results indicate that the overall networks for structure-from-motion and biological motion perception in the occipital and parietal lobe are not adult-like by the age of 6 years. Group differences were found in both studies when activation patterns of adults and children were compared. There was clear evidence that differences in neural development of visual perception can be linked to the dorsal stream. Adults showed neural specialization within dorsal brain areas, for structure-from-motion perception particularly in area V3a, whereas children activated both dorsal and ventral areas, with less apparent neural specialization. A similar pattern was found for biological motion processing. Adults mainly activated the dorsal stream and pSTS, which acts as a pivotal point between the dorsal and ventral stream, whereas children also showed activity within the ventral stream.

These data therefore provide evidence for maturation in the parietal lobule and are in line with general anatomical delayed development of the M-pathway in the dorsal stream including the parietal lobule, which showed that grey matter does not reach maturity by the age of 6 years (Braddick, Atkinson et al. 2003; Gogtay, Giedd et al. 2004; Sowell, Thompson et al. 2004).

Although the acquisition of skills in childhood appears to involve functional specialization within brain regions, little is known about the neural changes that support children's increasing cognitive efficiency. Nevertheless, the way in which maturation is expressed in neural activity in younger children is still under debate, and cannot be entirely solved here. Of course, fMRI in young children is very demanding because of the need for subject compliance. Studies with children younger than age 4 normally make sedation inevitable. Thus, most

visual fMRI studies in young children investigated the activity to unattended photic stimulation. One common finding reported in these studies is that the BOLD response in infants differs qualitatively from the adults BOLD signal (Yamada, N. et al. 1997; Born, Leth et al. 1998; Martin, Joeri et al. 1999; Marcar, Strassle et al. 2004), challenging the comparability of activity measured in infants and adults. Further work will be needed to describe the hemodynamic response in infants and young children, which in turn will help to gain more insights into the early development of function specific visual networks measured with fMRI.

## 8.2 Development of Dorsal and Ventral Stream Processing

Studies dedicated to the development of visual motion processing, have often considered their findings to represent more generally the developmental timeline of the dorsal stream. Likewise, developmental findings on color, texture or form processing have been assumed to represent the maturation of the ventral stream (Schrauf, Wist et al. 1999; Gunn, Cory et al. 2002; Mitchell and Neville 2004; Coch, Skendzel et al. 2005; Parrish, Giaschi et al. 2005). In this respect, our results might support the view that the dorsal stream develops more slowly than the ventral stream, consistent with results from behavioral (Schrauf, Wist et al. 1999; Gunn, Cory et al. 2002; Braddick, Atkinson et al. 2003) and electrophysiological studies (Crewther, Crewther et al. 1996; Mitchell and Neville 2004; Coch, Skendzel et al. 2005). However, there is also substantial evidence for a slower development of the ventral stream (Dobkins, Anderson et al. 1999; Gordon and McCulloch 1999). Why and if dorsal stream development is more protracted than the development of the ventral stream is still a matter of debate but the following remarks could add an explanation. It is commonly accepted that the later developing a brain system is, the more scope there is for postnatal environmental influence. This may be particularly important for components of the dorsal pathway that have to integrate information from sensory systems with propioceptive feedback to generate "body-centered" representations of action. As the body of the infant is developing physically, important factors such as length and weight of limbs continue to change. Thus, it may be more important to retain plasticity in the dorsal than in the ventral (see (Gilmore and Johnson 1997)) pathway. By the delaying aspects of the dorsal pathway, plasticity can be

retained for longer periods of time. However, there is a potential cost to this in that later developing systems tend to be more vulnerable to disruptions in development (Braddick, Atkinson et al. 2003). Thus, we anticipate that the dorsal visual stream should show more evidence of plastic changes following differences in experience in otherwise healthy children, but that the dorsal pathway will also show more evidence of deficits in some developmental disorders. These claims are discussed in chapter 10.

However, the investigation of the dual route visual processing paradigm has only recently been applied to the study of infant perceptual and cognitive development (Bertenthal, Proffitt et al. 1987; Atkinson 1992; Mareschal and Baker 1999) and many fundamental questions remain. Beside the question whether it is the dorsal or the ventral route that functionally develops first during infancy, another concerns whether there is increasing separation, or increasing integration, between the two pathway with development. Computational and behavioral evidence indicates that even when the dorsal route is functioning, there may be an initial lack of integration between the two pathways resulting in specific patterns of behavioral deficits. If integration or separation of the two pathways is a specific maturational marker of development can not entirely be answered in this thesis and remains to be answered in future studies. Of course, for effective visuo-cognitive and visuo-motor function, motion and form processing cannot operate in isolation from each other. Object motion must be perceptually bound to the identity of a recognized object, and motion yields information about 3D shape and biological characteristics which may make essential contributions to object recognition. The binding of motion to object identity has been the subject of much discussion in relation to the development of object permanence. Hopefully, studies of development in the future will be able to provide a neurobiologically based account of how dorsal- and ventral-stream information are integrated, and perhaps more sensitive tools for understanding developmental anomaly. More broadly, developmental understanding of detailed motion mechanisms has reached a level where we can consider their broader role in the development of functional vision.

# Outlook

## *8.3 Combining fMRI and DTI (diffusion tensor imaging): fMRI-guided DTI fiber tracking*

A powerful, non-invasive technique for estimating and visualizing white matter tracts in the human brain in vivo is white matter fiber tractography that uses magnetic resonance diffusion tensor imaging. We have also recorded DTI data of all subjects in the biological motion perception task and plan to perform a combined fMRI/DTI study, both to develop a setup for verifying fiber tracking results using fMRI-derived functional connections. First, an fMRI-based somatotopic map of ten regions of interest (bilateral V1, hMT+, FG, pSTS and two ROIs within the parietal cortex) will be reconstructed, based on fMRI activations that were provoked by biological motion perception tasks. Second, fMRI-guided DTI fiber tracking will be performed to generate DTI-based somatotopic maps, using a standard line propagation and an advanced fast marching algorithm. We expect that the results will illustrate that the combination of fMRI with DTI can supply additional information in order to choose reasonable seed regions for generating functionally relevant networks and to validate reconstructed fibers. These findings will also be particularly important for future studies with clinical populations such as developmental delays in e.g. VLBW children (see chapter 8.4).

## *8.4 Investigating Motion Perception in VLBW Children*

In a current project, we aim to investigate neural mechanisms underlying potential developmental disorders of very low birth weight (VLBW) adolescents. Previous approaches in developmental and diagnostic magnetic resonance imaging (MRI) of children have focused on structural brain development as a fundament for cognition. In this project we aim to investigate neural mechanisms underlying visual-cognitive development using functional magnetic resonance imaging (fMRI). The correlation between brain activity and clinical assessment parameters in VLBW adolescents will contribute to the understanding of the relationship between visual task performance, brain specialization, detailed neurodevelopmental assessment as well as motor performance. The neuroimaging experiments include the structure-from-motion as well as the

biological motion task and additionally a task in which animals and tools have to be recognized.

There is strong evidence that the dorsal stream is more vulnerable and needs more cortical feedback than the ventral stream, which has been described in children aged 4 years and older (Braddick, O'Brien et al. 2001). In these children the parsing of the visual array into globally organized forms appears to develop more securely than the equivalent parsing by relative motion. These developmental changes may reflect a learning- and experience-based fine-tuning of visual recognition processes. The integration of local motion into the perception of coherent translational motion is a basic integrative process of the motion pathway for which norms of behavioral performance in the 4-10 year age range are already established (Gunn, Cory et al. 2002; Parrish, Giaschi et al. 2005), and which have also been shown to be sensitive to neurodevelopmental disorders (Braddick, Atkinson et al. 2003). Recent findings, however, animated the unresolved debate on the neural mechanisms underlying the development of motion processing. For example, our group recently reported imaging data showing that full development of coherent motion in MT+ is not reached until adolescence (Bucher, Dietrich et al. 2006). Tasks inducing dynamic visual adaptation and action based upon the visual dynamic stimulus require even stronger cognitive demands. It has been shown that these functions mature until adolescence (Schrauf, Wist et al. 1999). Recent studies suggest that the late maturation depends on development of parietal lobule functions. Particularly, lesions in periventricular cortex were associated with delayed development in adolescents (Pavlova, Staudt et al. 2003; Pavlova, Sokolov et al. 2005; Pavlova, Sokolov et al. 2006). It is however, unclear whether the latter processes may be delayed in VLBW children with and without apparent sonographic periventricular lesions. VLBW children are a population at risk for neurodevelopmental impairments. Moderate to mild intellectual impairments occur rather frequently and visuomotor skills are often impaired in this population (Goyen, Lui et al. 1998; Foulder-Hughes and Cooke 2003; Seitz, Jenni et al. 2006). In addition, visuomotor difficulties have been associated with deficits in fine motor performance (Goyen, Lui et al. 1998), whereas certain motor tasks correlate with visuomotor performance of intellectual performance (Seitz, Jenni et al. 2006). Thus, delayed maturation in visuo-perceptual and visuomotor processing may be related to deficits in parietal lobule functions. However, it is unclear which neural

mechanisms contribute to visuomotor impairments in VLBW children and whether these mechanisms support specific parts of the visuomotor system, such as the visuo-perceptual input, motor output or intermediate processes between input and output such as the visuomotor transition.

The findings of this study enable a better counseling of parents and VLBW children regarding the spectrum and mechanisms of potential in visuo-perceptual and visuomotor deficits that influence school performance. Learning strategies may be tailored according to these findings.

# 9 Curriculum vitae

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**EDUCATION**

| | |
|---|---|
| 1996 | High school graduation |
| 1996 – 2003 | Study of Psychology at the University of Zurich,1. Subsidiary Subject: Children and Youth Psychopathology; 2. Subsidiary Subject: Neurophysiology |
| September 1998 – June 1999 | Socrates-Erasmus Exchange Program at the University of Keele, Great Britain |
| December 2002 | Diploma thesis: Perceptual anticipation of dynamic and kinematic events with or without sensumotoric experience (unpublished diploma thesis) |
| March 2003 | College graduation |
| Since April 2004 | Ph.D Student and scientific assistant at the MR Center, University Children's Hospital, Zurich, Prof. E. Martin-Fiori |
| April 2008 | Doctoral examination |
| April 2008 - | Postdoctoral Fellow at the MR Center, University Children's Hospital Zurich, Prof. E. Martin-Fiori |

**PRACTICAL EXPERIENCE**

| | |
|---|---|
| March 1997 – June 1997 | Research assistant at the Psychology Department, University of Zurich |
| April 1999 – January 2001 | Research assistant at the Psychology Department, Developmental Psychology University of Zurich |

| | |
|---|---|
| April 2001 | Private lesson teacher for Neurophysiology at the School for Occupational Therapy; Zurich |
| September 2001 - February 2002 | Tutor for Neurophysiology at the Psychology Department, University of Zurich |
| July 2002 – October 2002 | Internship at the Charité, Hospital of Psychiatry, Psychosomatic Medicine and Psychotherapy for Children and Youth, Berlin |
| April 2003 – June 2003 | Internship at the Neurological Clinic, University Hospital, Department of Neuropsychology, Zurich |

**OWN PUBLICATIONS**

**PUBLICATIONS (published or peer-reviewed)**

Klaver P, ***Lichtensteiger J***, Bucher K, Dietrich T, Loenneker T, Martin E. (2008). Dorsal stream development in motion and structure-from-motion perception. Neuroimage., 39(4):1815-1823. Epub 2007 Nov 22.

***Lichtensteiger J***, Bucher, K, Loenneker, T, Martin, E, Klaver, P. The role of dorsal and ventral stream development in biological motion perception. *[submitted manuscript]*.

**ABSTRACTS & POSTERS**

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# 10 Appendix

## Die Entwicklung visueller Fähigkeiten

### bei Kindern im Vorschul- und Schulalter

### (4-7 Jahre)

**Die Studie steht unter der Leitung und Verantwortlichkeit von:**

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KINDERSPITAL ZÜRICH
Universitäts-Kinderkliniken · Eleonoren-Stiftung

**Die Entwicklung visueller Fähigkeiten bei Kindern im Vorschul- und Schulalter**

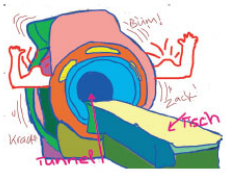
**http://www.kispi.unizh.ch/mr**

**Wer sind wir?**

Wir sind eine Forschergruppe an der **Universitäts-Kinderklinik (Kinderspital) Zürich.** Unser Interesse gilt der Entwicklung höherer visueller Fähigkeiten im Kindesalter. Diese Entwicklung findet vor allem in den ersten Lebensjahren statt, deshalb können wir Untersuchungen nur an Kindern im Vorschul- und Schulalter durchführen. Um solche Untersuchungen realisieren zu können, brauchen wir Ihre Unterstützung und die Unterstützung Ihres Kindes.

**Welches sind die Ziele dieser Studie?**

Während der Entwicklung finden im kindlichen Gehirn als direktes und normales Resultat von Lernprozessen strukturelle und funktionelle Änderungen statt. Es ist für uns wichtig, diese entwicklungsbedingten Änderungen im Gehirn zu verstehen, da wir somit auch Lern- und Reifungsprozesse besser verstehen – sowohl





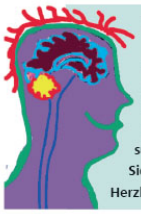
erfolgreiche, wie auch weniger erfolgreiche. Die Verarbeitung visueller Information wird zudem von kognitiven Prozessen begleitet. Das Erkennen von bewegten Objekten z.B. kann somit gut die geistige Entwicklungsstufe eines gesunden Kindes widerspiegeln oder im Vergleich mit gleichaltrigen Kindern eine mögliche Entwicklungsverzögerung aufzeigen. Um bei einem Kleinkind eine Entwicklungsverzögerung besser diagnostizieren und verstehen zu können, benötigen wir für einen Vergleich **eine Gruppe von gesunden Kindern** und somit Ihre Unterstützung. Um derartigen Fragen auf den Grund zu gehen, verwenden wir ein bildgebendes Verfahren, die sogenannte **funktionelle Magnetresonanztomographie,** oder kurz fMRI (functional magnetic resonance imaging). Mit dieser Methode ist es möglich, die Vorgänge im Gehirn direkt zu beobachten, während eine Person z.B. Objekte beobachtet. Diese moderne Untersuchungstechnik ist mit keinerlei Strahlenbelastung, Schmerzen oder Spritzen (es wird kein Kontrastmittel benötigt) verbunden, sondern erzeugt Bilder aus Magnetfeldern und Radiowellen.

**Wie läuft die Untersuchung ab?**

Während der fMRI Untersuchung werden dem Kind über eine Videobrille verschiedene sich bewegende oder statische Objekte zur visuellen Verarbeitung präsentiert. Vor der eigentlichen Messung wird dem Kind ausserhalb des Tomographen alles erklärt. Danach fängt die eigentliche Messung im Tomographen an, die etwa 1/2 Stunde dauert. Um die so erhobenen Daten mit Daten von Kindern zu vergleichen, welche zu früh geboren wurden, ist es wichtig, dass bei Ihrem Kind noch zusätzlich Tests zum Sehvermögen und zu kognitiven Fähigkeiten durchgeführt werden. Diese können aber auch bei Ihnen zu Hause durchgeführt werden.

**Welche Untersuchungsmethode wenden wir an?**

Wir messen die Hirnaktivität, während das Kind die Objekte beobachtet. Die ganze Sitzung dauert insgesamt ca. 1 Stunde. Wir zeigen und erklären Ihnen und Ihrem Kind gerne die so entstandenen Bilder des Gehirns. Die Bilder dürfen Sie gerne mit nach Hause nehmen, ein Arzt wird sie bei uns anschliessend noch kontrollieren. Als Dankeschön für die Mitarbeit erhält jedes Kind eine kleine Belohnung in Form einer Hör-CD.



**Falls Sie sich und Ihr Kind gerne anmelden möchten, können Sie dies gerne direkt per Mail oder Anruf tun. Sie können auch den beiliegenden Talon ausfüllen und an obenstehende Adresse senden. Für weitere Informationen stehen wir Ihnen natürlich jederzeit zur Verfügung. Auf unserer Homepage (www.kispi.unizh.ch/mr) haben Sie und Ihr Kind die Gelegenheit, sich einen Untersuchungsablauf anhand eines Comics anzuschauen. Bitte melden Sie sich bitte bei allfälligen Fragen ebenfalls bei der Kontaktperson. Herzlichen Dank für Ihr Interesse!**

Die Studie „Entwicklung der visuellen Fähigkeiten im Vorschul- und Schulalter" untersucht, wie sich unser Gehirn entwickelt und wie es lernt. Gesucht werden Kinder im Alter von 4 – 7 Jahren (mit gutem Sehvermögen, ohne neurologische Erkrankungen). Gemessen wird die Hirnaktivierung mit Hilfe der funktionellen Magnetresonanztomographie. Dies birgt keine Risiken und dauert ca. 1 Stunde. Die Kinder erhalten einen Einblick in die aktuelle Forschung, Bilder vom Hirn und ein kleines Geschenk in Form einer Hör-CD. Gerne schicken wir Ihnen weiteres Informationsmaterial zu unserer Studie.

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Natel

Mail

Name des Kindes

Vorname des Kindes

Geburtsdatum

Geschlecht: ☐ m ☐ w

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Geschlecht: ☐ m ☐ w

**Figure 12: Broschure for parents' and childrens' information distributed prior to investigation**